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DISTRIBUTION, HABITAT REQUIREMENTS, AND LIFE HISTORY OF THE BLACK-CAPPED VIREO (*VIREO ATRICAPILLA*)¹

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INTRODUCTION

A study of the black-capped vireo (*Vireo atricapilla*) was made to learn more of this little known species and to explain its restricted and localized distribution. To determine its past and present distribution, records in the literature, observations of others, and a survey of the limits and center of the breeding range in Oklahoma, Texas, and Mexico (made by the author and Richard R. Graber in 1954-56) were used. The wintering grounds in Sinaloa and Nayarit were examined in 1955. The vegetation and climatic aspects of the habitat were studied. An intensive study of the habits and life history was made in Oklahoma and in Texas in 1955-56.

I wish to thank George M. Sutton of the University of Oklahoma for his aid and guidance, the many persons who gave me information concerning the species, the landowners who allowed me to work upon their properties, and Richard R. Graber who assisted me in all phases of this study. Plant specimens were identified by George J. Goodman of the University of Oklahoma, B. L. Turner and W. I. McCart of the University of Texas, and Rogers McVaugh of the University of Michigan. Insect remains in stomachs were identified by Milton W. Sanderson of the Illinois State Natural History Survey. Financial aid was furnished by the National Science Foundation

(fellowship 1955-56), and the Womens Garden Clubs of America (sponsor, Norman, Oklahoma, Chapter).

DISTRIBUTION

GENERAL

The black-capped vireo is limited in its breeding to the south central United States and north central Mexico. It occupies an area in which eastern floral and faunal elements meet with western, and northern with southern—an area of hybridization and intergradation. Furthermore, the special habitat chosen by the bird is in itself intergrading and transitional and therefore very localized within the area.

Sight records and one specimen place the northernmost point of occurrence (as an accidental summer visitant) in southeastern Nebraska (Brunner 1896). The species has been known to breed as far north as central Kansas but, although Tordoff (1956) lists two sight records in recent years, the status of the species in this state is uncertain. I visited localities in which the black-capped vireo had been found breeding and failed not only to find the species, but also to find any habitat comparable to that now occupied by the birds in other areas. I believe that land use (overgrazing) and climatic conditions (drought) have made the former habitat in southern and southwestern Kansas unacceptable. The northernmost breeding area I have found is in northern Oklahoma (Major County).

¹ Based on a thesis presented in partial fulfillment of the requirements for the Doctor of Philosophy degree at the University of Oklahoma, Norman, Oklahoma.

The southernmost known breeding grounds are in central Coahuila, Mexico (Sierra Madera, east of Ocampo). This is also the western limit of breeding (103° W. Long.). The eastern limit is at approximately 97° W. Long. (Tulsa, Oklahoma, and Dallas, Texas).

The species winters along the west coast of Mexico from the foothills (at least as high as 2700 feet) of the Sierra Madre Occidental to the coast (Mazatlan, elevation 10 feet), from southern Sonora to Jalisco and Michoacan, and probably farther south. There are two records from Guerrero and one from Campeche. Observations by collectors for Dr. Robert T. Moore, by Dr. Allan R. Phillips, and by myself indicate that southern Sinaloa and Nayarit are the center of the wintering grounds. I saw more birds in Nayarit than in southern Sinaloa—as many as three in a linear mile in a morning near Las Varas, Nayarit. Dr. Moore wrote me that though he had material from about the same number of collecting stations in Nayarit, Jalisco, Durango, and Sinaloa, about five times as many specimens had come from Sinaloa as from the other states.

A detailed list of distributional records is given in the thesis. A map of these records is presented here (Fig. 1).

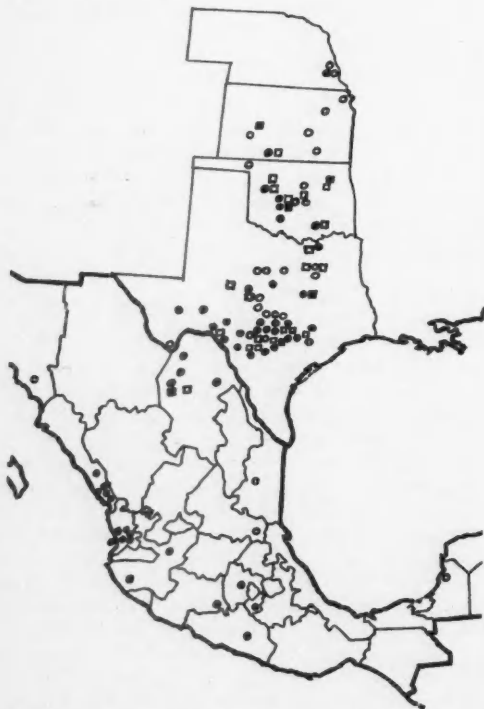


FIG. 1. Map showing distribution of *Vireo atricapilla*. Solid circles represent specimens; solid squares, nests, eggs, or juveniles in collections; hollow squares, reported breeding; hollow circles, reported occurrence (records from 1852 to 1956).

OKLAHOMA

At the time of this study, the black-capped vireo was found breeding in Caddo, Dewey, and Major counties. It was observed in Blaine and Canadian counties and it very likely breeds in these counties. It has been seen in Beaver, Cleveland, and Payne counties in summer, and may occasionally breed in the latter two, as well as in Oklahoma county.

The species has not been reported from Creek or Tulsa counties for over twenty years. I saw what looked like suitable habitat in the eroded sandstone hills of this region but did not have time to search the area to my satisfaction. Despite a thorough search, the species was not found in Comanche and Murray counties. In both counties, the areas in which the bird was found have been much disturbed. Special effort was made to find the species in Woodward, Woods, and Alfalfa counties, but none was seen there.

TEXAS

The black-capped vireo has been found locally throughout central Texas. The center of its distribution there lies in the hill country and Balcones Escarpment, an oak-cedar covered marginal portion of the Edwards Plateau. As far as I have been able to determine, the bird breeds no farther west than Devil's River in northwestern Valverde County and no farther south than central Uvalde County. In the southeast, the breeding range follows the line of the Balcones Escarpment through northern Bexar, eastern Comal, eastern Hays, and eastern Travis counties. Suitable habitat becomes sparse and spottily distributed north of the San Saba and Colorado Rivers. In fact, the only recent records in northern Texas are from southwestern Dallas and northeastern Ellis counties.

To check reports of the species from eastern Texas in the "Big Thicket" area, I visited the eastern edge of this area which lies between the Trinity and Sabine Rivers south of Nacogdoches. I did not see any vegetation that was anything like that which the bird now occupies in other areas. Until specimens are taken in this region, I regard such reports as dubious. I have corresponded with several observers from Houston and none has ever seen the bird in the area, although Selle (1933, 1934) lists it in his books covering the Houston area (including the Big Thicket).

The species appears to have suffered severe reduction in numbers in the Trans-Pecos country and along the western edge of the Edwards Plateau. I made careful searches for the bird and for habitat that might attract it in the Davis, Chisos, and Glass mountains, and in Terrell, Crockett, western Valverde (Pecos River Gorge), Reagan, western Irion, Schleicher, Sutton, western Kimble, and San Angelo counties.

For years the gorge near the mouth of the Pecos River has been occupied by black-capped vireos, but I could find none there in 1955 and 1956. A flood scoured the vegetation from the lower portion of the

canyon in 1954, and drought had killed most of the scrubby growth on the upper slopes. This shrubbery appeared to have been suitable habitat in earlier years, but in 1955 and 1956 stood dead and bare. In Ligon Canyon in Terrell County the same conditions prevailed. In the Chisos Mountains, half or more of the trees and shrubs living at the 5000-6000 ft level, in 1955, were dead in 1956. The hillsides between Junction and Ozona had innumerable dead cedars and some dead oaks on them, all apparently killed by the drought.

Near Weatherford, Parker County, and through Palo Pinto and Stephens counties to Breckenridge there is some hilly terrain covered with cedar-oak growth that might offer suitable habitat. This sort of habitat also extends into southeastern Graham and southern Jack counties. I did not find any black-capped vireos at Possum Kingdom Lake. I did not check elsewhere in this area.

A set of eggs allegedly collected in Cameron County, Texas, may or may not have been taken there. Baird (1874) lists Woodhouse's type as from El Paso—surely an error. There is no other record of the bird from El Paso.

MEXICO

The first breeding record for Mexico is one by Renardo (1886) who wrote only that he found it breeding in the Rio Grande Valley. Specimens taken in the Sierra del Carmen (Miller 1955) and the Sierra del Pino (Van Hoose 1955), which lie to the north of Ocampo, Coahuila, probably represent breeding populations. The Sierra del Pino extends into Chihuahua so the species may breed in the eastern part of that state. In June of 1956, I found nesting black-capped vireos in two small mountain chains (Sierra Padilla and Sierra Madera) about Ocampo in central Coahuila. Five nests were found.

I was not able to check the Sierra de los Alamitos or the Sierra de la Palma, both of which are a little south of the area in which I found the birds. I attempted to find the species in the mountains about Saltillo, still farther south. Here at 6500 feet, but not at lower elevations, there was some oak chaparral, but I did not find the vireos.

I looked for the species also in the mountains south and southwest of Hidalgo del Parral. I went first to San Francisco, then south in northwestern Durango through Rancho Blanco and Bojito (not on any maps in my possession including a U. S. Air Force aeronautical chart with a 1:1,000,000 scale) to the head of the Rio Verde (at the Continental Divide) and as far up into the mountains as a place called Las Flores, which lies between 9000 and 10,000 feet elevation and at which there are magnificent growths of pine. I particularly searched oak chaparral covered slopes lying just below the level of Pinyon pine (about 5500 feet). I chose this area because it lies directly between the breeding grounds and the wintering grounds, and at the head of some of the rivers that lead to large barrancas through which black-capped vireos may be channeled in migration

(Moore 1938). It appears that the species must pass through this region, and if suitable habitat exists, it may stay to breed. However, I did not find it. The chaparral of the lower, warmer slopes had been largely destroyed by overgrazing and drought. That which might have been adequate on the upper slopes was probably at elevations too high for this species. Certain isolated areas may be suitable, but since few roads are passable in this region these areas may well remain undiscovered for some time.

The record from Santa Leonor, Tamaulipas (Phillips 1911) suggests that the black-capped vireo may breed on the eastern slopes of Sierra Madre Oriental west of Ciudad Victoria, but to date no one has discovered it there. I have passed through Ciudad Victoria a number of times and have thought that the shrubby growth along the highway south of this city resembled that of the wintering grounds more than that of the breeding grounds. This record (if valid) may simply be one of accidental occurrence, a migrant that wandered astray.

Non-breeding birds have been found in Mexico between August 27 and March 20, and possibly can be found in April. Scattered locality records in September and March probably represent migrants, the rest, wintering birds. Moore (1938) has suggested that the black-capped vireo follows the Mexican plateau to the heads of river gorges leading westward to the coast, thus enabling it to by-pass the higher altitudes of the Sierra Madre Occidental. This well may be the case since this route is the shortest between the wintering and breeding grounds and it offers a way through at least some habitat not unlike that in which the bird winters and breeds. However, scattered records also indicate that it is possible for the bird to pass over the mountains. One was taken at 9500 feet elevation on Volcan de Toluca.

HABITAT

FACTORS AFFECTING THE VEGETATION OF BREEDING AREA

The black-capped vireo breeds in scrubby tree growth of the forest-grassland ecotone in the area of transition between Austroriparian and Sonoran biotas (in the Balconian and Texan Provinces of Blair 1950). The extent and height of this dwarf forest habitat is largely determined by climatic, edaphic, and topographical factors, but is also affected by secondary factors like fire, grazing, and human disturbance.

Along the northern and western edge of the range suitable habitat occurs in ravines which provide more mesic conditions than the prairie upland. On the eastern edge of the range weathered and eroded highlands and stream boundaries (above the flood plains) provide edaphic conditions for suitable vegetation. Southward the habitat occupies hilltops and mountain slopes to over 6000 feet. Thus the black-capped vireo has been found in prairie ravines in Kansas, in canyons like that of the Pecos River in western Texas, on eroded sandstone slopes in Okla-

homa, on the hills of the Edwards Plateau, and on mountainsides in Brewster County, Texas, and in central Coahuila, Mexico.

Areas supporting a climax unsuitable chiefly because of size and stand are rendered satisfactory by fire and cutting of trees. I have found black-capped vireos so often on burns that I am convinced that the burning practiced by the Indians of the plains probably aided in the dispersal of this species. In recent times man has provided habitat by chopping down large trees, for example, the cedars of the Texas hill country which have formed brakes so dense no shrub understory could develop.

Overgrazing has aided weathering and erosion so that coarse soils favoring scrub growth have replaced richer grassland soils. Browsing by goats, which have been introduced in numbers in Texas within the last half century, reduces the habitat. Deer browse does not bother the bird. Nests are frequently placed in cedar and evergreen sumac (*Rhus virens*) in overgrazed pastures, as these plants are not eaten by cattle which do browse on small live oaks (*Quercus virginiana*).

Human population pressure can directly affect the black-capped vireo. *V. atricapilla* is not a solitary species; a population consisting of five males and three females is the smallest breeding population I have ever found. Since each pair requires about three to four acres, it appears that a minimum of approximately 10-12 acres of suitable habitat is required for the bird to become established in any one place. This is more than is generally given to native shrub growth near any human dwelling.

ASSOCIATED SPECIES OF BIRDS

Birds which occupied the same habitat as the black-capped vireo in Oklahoma were the bobwhite (*Colinus virginianus*), mourning dove (*Zenaidura macroura*), yellow-billed cuckoo (*Coccyzus americanus*), roadrunner (*Geococcyx californianus*), chuck-will's-widow (*Caprimulgus carolinensis*), poorwill (*Phalaenoptilus nuttallii*), downy woodpecker (*Dendrocopos pubescens*), Carolina chickadee (*Parus carolinensis*), tufted titmouse (*Parus bicolor*), Bewick's wren (*Thryomanes bewickii*), blue-gray gnatcatcher (*Poliophtila caerulea*), Bell's vireo (*Vireo bellii*), black-and-white warbler (*Mniotilta varia*), prairie warbler (*Dendroica discolor*), yellow-breasted chat (*Icteria virens*), cowbird (*Molothrus ater*), cardinal (*Richmondia cardinalis*), blue grosbeak (*Guiraca caerulea*), painted bunting (*Passerina ciris*), lark sparrow (*Chondestes grammacus*), and field sparrow (*Spizella pusilla*).

In Texas, the mourning dove, ground dove (*Columbigallina passerina*), ladder-backed woodpecker (*Dendrocopos scalaris*), black-crested titmouse (*Parus atricristatus*), Bewick's wren, mockingbird (*Mimus polyglottos*), blue-gray gnatcatcher, white-eyed vireo (*Vireo griseus*), Bell's vireo, yellow-breasted chat, cowbird, cardinal, painted bunting, house finch (*Cardinalis mexicana*), rufous-crowned sparrow (*Aimophila ruficeps*), lark sparrow, and field sparrow were

found in the same area as the black-capped vireo. In some localities the scrub jay (*Aphelocoma coerulescens*), black-and-white warbler, golden-cheeked warbler (*Dendroica chrysoparia*), and black-throated sparrow (*Amphispiza bilineata*) were found in the black-capped vireo's habitat.

In Mexico (Coahuila), the mourning dove, ladder-backed woodpecker, scrub jay, bush-tit (*Psaltriparus minimus*), Bewick's wren, mockingbird, gnatcatcher, black-headed grosbeak (*Pheucticus melanocephalus*), house finch, Mexican goldfinch (*Spinus psaltria*), rufous-sided towhee (*Pipilo erythrophthalmus*), and rufous-crowned sparrow occupied the black-capped vireo's habitat.

Although the ecological niches of the black-capped, Bell's and white-eyed vireos meet and overlap slightly, there apparently is no aggression in their competition. I never witnessed any fighting between black-capped and white-eyed vireos whose territories clearly overlapped, or between Bell's and black-capped vireos on overlapping territories. Bunker (1910) reported finding a nest of the Bell's vireo and one of the black-capped vireo in the same bush. The two species (I have never seen overlapping of territories of all three species, though all three can be found in one locality and in such a locality territories of two of the three may overlap) appear to ignore each other, each going about its daily activities as if the other were not present. I found no evidence of interbreeding between these species.

The habitats of Hutton's vireo (*Vireo huttoni*) and the gray vireo (*V. vicinior*) differ more from that of the black-capped vireo than do those of the Bell's and white-eyed vireos. In Coahuila, Mexico, these five vireos separate nicely into different levels and habitats. The Bell's occupies the mesquite lowlands between the mountains; the white-eyed, more mesic lowlands; the gray, juniper (*Juniperus monosperma*) lowlands and low hillsides; the black-capped, slopes at 3000 to 5000 feet covered with low oak mottes; the Hutton's, the pinyon and pine level above that of the black-capped. The Hutton's and gray are western in distribution, meeting the black-capped at the eastern edge of their range. The white-eyed is more eastern in its distribution, meeting the black-capped at the western edge of its range. The Bell's has a wide, somewhat central, distribution.

SPECIES OF WOODY PLANTS IN BREEDING HABITAT

From north to south the plant species forming the habitat gradually change. In the northern and eastern parts of the bird's range (Oklahoma, and northern and eastern Texas) predominant tree species are the blackjack oak (*Quercus marilandica*), post oak (*Q. stellata*), and red cedar (*Juniperus virginiana*). In the central part (Texas hill country), they are live oak (*Q. virginiana*), Spanish oak (*Q. texana*), and mountain cedar (*J. ashei*). In the southwestern part, they are various scrub oaks (probably *Q. undulata*, *Q. texana* or *gravesii*, *Q. mohriana*, *Q. grisea*, *Q. intricata*, and others), yuccas (*Yucca* sp.), and cornaceous shrubs (*Garrya* sp.). Junipers are few

in the habitat in Coahuila, Mexico. Various kinds of sumac (*Rhus* sp.) are important constituents of the habitat everywhere.

Woody plants now growing in parts of Comanche County, Kansas, believed to have been inhabited by the vireo some years ago, include the red cedar, American elm (*Ulmus americana*), gray dogwood (*Cornus drummondii*), sumac (*Rhus glabra*, *Rhus trilobata*), poison ivy (*Rhus toxicodendron*), grape (*Vitis* sp.), woodbine (*Parthenocissus quinquefolia*), chinaberry (*Sapindus drummondii*), plum (*Prunus* sp.), currant (*Ribes* sp.), lead plant (*Amorpha canescens*), wafer ash (*Ptelea trifoliata*), and walnut (*Juglans nigra*). A few oaks (*Q. stellata*, *Q. muhlenbergii*, and *Q. macrocarpa*) occur in some ravines, but they are too large and too scattered to afford the type of growth preferred. The bird probably occupied ravine slopes which were covered with small trees and shrubs of the species listed above. This type of habitat has been destroyed by drought and cattle on all but the steepest and most shaded slopes.



FIG. 2. Habitat in northern part of breeding range. Blackjack oak-post oak-red cedar covered canyon slopes. Photo taken May, 1954, in Caddo County, Oklahoma.



FIG. 3. Height of vegetation in well-populated, breeding habitat. Photo taken May, 1955, Caddo County, Oklahoma.

The Kansas type habitat merges in northern Oklahoma with the cedar-oak (sometimes only oak; Figs. 2, 3) habitat so characteristic in that area and extends southward into northern Texas. The species

and their relative importance are indicated in a detailed description of my study areas which follows. Mr. Geth Osborne and Mr. Edward C. Fritz describe the habitat on limestone stopes in Dallas County, Texas, as secondary growth consisting of the following species: red cedar, post oak, turkey oak, red oak, live oak, green ash, sumac (*Rhus trilobata* and *R. glabra*), deciduous holly (*Ilex decidua*), poison ivy (*R. toxicodendron*), black haw (*Viburnum* sp.), *Forestiera* sp., *Prunus* sp., woodbine, and cactus (probably *Opuntia* sp.).

The Oklahoma-type habitat merges with that of the Edwards Plateau at about the latitude of Dallas as shown by the appearance of live oak. Relicts of the Edwards Plateau vegetation occur in the Arbuckle Mountains of southern Oklahoma. Post oak, blackjack oak, and cedar (the Oklahoma type habitat) occurs in the cross timbers as far south as Bastrop County, Texas, and are found in the central igneous region of Texas (Llano and surrounding counties).

The habitat on the Balcones Escarpment of the Edwards Plateau (Fig. 4) merges in Uvalde County with that occupied by the bird in the southwesternmost portion of its range. Trees and shrubs typical of the Edwards Plateau occur as far west as northeastern Terrell County (Webster 1950). Species typical of the oak chaparral of Brewster County were found in Uvalde and Kinney Counties. Sotol (*Dasylirion texanum*) and Mexican persimmon (*Diospyros texana*), prominent plants in the habitat in Coahuila, Mexico, are found on the Balcones Escarpment. The western limits of the black-capped vireo appear to coincide with the eastern limits of the gray oak (*Quercus grisea*) and oneseed juniper (*Juniperus monosperma*), though I do not believe that this vegetation itself halts the vireo. The character of the vegetation does appear to limit the eastern spread of this bird, for the mesic forests of the eastern United States do not provide growth of the right size and arrangement.

In southern Texas (Uvalde County), I found black-capped vireos occupying a habitat (burned over about seven years before) composed of the fol-

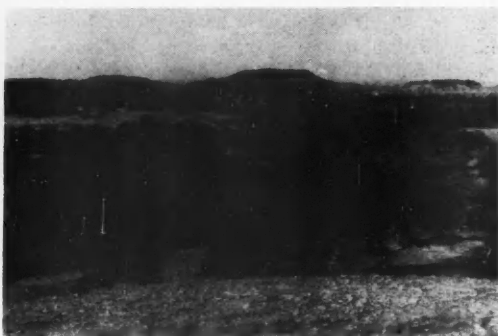


FIG. 4. Live oak-cedar, breeding habitat in Edwards Plateau. Photo taken May, 1956, at El Rancho Cima, Comal County, Texas.

lowing species: Mexican persimmon, mesquite (*Sophora secundiflora*), guajillo (*Acacia berlandieri*), buckthorn (*Rhamnus caroliniana*), evergreen sumac, leatherplant (*Jatropha spathulata*), algerita (*Berberis trifoliata*), and two chaparral oaks (*Quercus* sp.). A few larger trees of Spanish oak, live oak, and Mexican cedar (remnants of the dominant vegetation) were also present.

The habitat in northern Kinney County, Texas, appeared to be similar to that in the Glass Mountains north of Marathon. Cedar, scrub oak, live oak, mesquite, and evergreen sumac were major components. A few small pinyon pines (*Pinus cembroides*) and gray oaks were noted. In parts of the Glass Mountains these last named species are common in the scrub growth. The vegetation of the Glass Mountains has been described by Sperry & Warnock (1941).

The habitat in northern Terrell County, Texas, has been described by Webster (1950). The vegetation of the slopes is like that of the upper slopes of the Pecos River gorge, with the exception of cedars which are not found in the latter area. The persimmon-shin-oak association appears to have provided suitable habitat, as well as the cedar-shin-oak association in which the black-capped vireo was found by Thornton (1951). The cedar in the canyon floors is the habitat of the gray vireo, a very common species here. Terrell, Brewster, Kinney and southern Valverde counties are marginal areas for the black-capped vireo. In times when the climate is favorable these areas provide a habitat, but in periods of drought they do not.

The habitat in Sierra Padilla, Coahuila, Mexico, appeared to be very similar to that described by Lesueur (1945) for isolated limestone Sierras (especially Sierra del Pino) in northeastern Chihuahua. According to Lesueur the lowest oaks appear at 5600 feet, and grow in dense mottes about one meter high. The drooping juniper (*J. flaccida*) begins at 5800 feet. From 6200 to 6600 feet a dwarf form of *Quercus undulata* is common and with *Ceanothus greggii*, *Garrya obovata*, *Fendlera linearis*, *Juniperus flaccida* forms an impassable mat. I also noted in the area occupied by black-capped vireo *Acacia berlandieri*, *Cercis* sp., *Dasyllirion texanum*, *Yucca* sp., *Rhus virens*, *Mimosa* sp., *Quercus gravesii*, and *Quercus grisea*. A few large pines grew on isolated ridges in this range, but I saw no pinyon pines. In this area *Vireo atricapilla* was the common vireo. I saw only one other vireo, a Hutton's vireo.

The habitat in the Sierra Madera in Coahuila was similar to that of Sierra Padilla, but I saw no redbud (*Cercis* sp.) there, and a fine pine forest covered the higher slopes. This range reminded me of the Chisos Mountains, and of the Sierra del Carmen, as described by Miller (1955). Black-capped vireos were found only on dry, limestone hillsides where there were thick mats of vegetation about three to five feet in height. In this growth, *Quercus undulata* and *Rhus virens* were the most common woody plants. Also noted were: *Nolina* sp., *Yucca* sp., *Dasyllirion*

texanum, *Juniperus flaccida*, *Prunus* sp., *Rhamnus* sp., *Garrya* sp., *Lonicera* sp., *Bumelia* sp., and *Arbutus texana*. This shrub growth was most luxuriant on slopes facing north and east. That which I examined on other slopes appeared to be half-dead from the drought. There was no surface water in this range. The closest water, a small reservoir which supplied a few families, was two miles from the Sierra's base. The same situation existed at Sierra Padilla.

ARRANGEMENT OF WOODY PLANTS IN BREEDING HABITAT

The woody plants are principally small, many-branched trees and shrubs that provide good cover near the ground. Some larger trees grow in the habitat. This unevenness of vegetation is characteristic. I have never found the black-capped vireo in oak shinnery cover of uniform height. The species prefers mottes which because of their distribution in small thickets or clumps with spaces between give the landscape a "woolly" aspect when viewed from a distance.

The total number of shrubs and trees in a 50 ft-square quadrat varied from 33 to 328 (average 122.3) in the Oklahoma study area. In Texas, the number ranged from 61 to 568 (average 246). In one quadrat in Mexico (Sierra Padilla) the number was 715.

There was a considerable variety of woody plants (Tables 1, 2). No fewer than 27 species of such plants grew in the Oklahoma quadrats. The average number of species per quadrat was 7.8 (maximum number, 16; minimum, 4). In all the Texas quad-

TABLE 1. Frequency (In Percent) of Woody Plants in Oklahoma Quadrats.

Species	Fifty-two Caddo Co. quadrats
<i>Quercus marilandica</i>	98.0
<i>Juniperus virginiana</i>	92.3
<i>Quercus stellata</i>	90.3
<i>Celtis reticulata</i>	73.0
<i>Opuntia</i> sp.....	67.3
<i>Rhus glabra</i>	63.4
<i>Symphoricarpos orbiculatus</i>	59.6
<i>Aesculus glabra</i>	44.2
<i>Rhus toxicodendron</i>	30.7
<i>Parthenocissus quinquefolia</i>	28.8
<i>Cercis canadensis</i>	21.1
<i>Quercus muhlenbergii</i>	19.2
<i>Bumelia lanuginosa</i>	19.2
<i>Prunus angustifolia</i>	15.3
<i>Rhus trilobata</i>	15.3
<i>Ulmus americana</i>	9.6
<i>Cornus drummondii</i>	7.6
<i>Juglans nigra</i>	5.7
<i>Smilax bona-nox</i>	5.7
<i>Amorpha canescens</i>	3.8
<i>Yucca glauca</i>	3.8
<i>Prunus mexicana</i>	1.9
<i>Morus rubra</i>	1.9
<i>Ptelea trifoliata</i>	1.9
<i>Forestiera pubescens</i>	1.9
<i>Cissus incisa</i>	1.9
<i>Vitis</i> sp.....	1.9

TABLE 2. Frequency (In Percent) of Woody Plants in Texas Quadrats.

Species	THIRTY-FIVE QUADRATS IN HAYS AND COMAL COUNTIES	
	Fourteen quadrats in recently burned area	Twenty-one Hill Country quadrats
<i>Quercus virginiana</i>	100.00	90.4
<i>Juniperus ashei</i>	64.2	90.4
<i>Diospyros texana</i>	85.7	66.6
<i>Rhus virens</i>	35.7	95.2
<i>Quercus texana</i>	92.8	38.0
<i>Berberis</i> (both <i>trifoliata</i> and <i>swazeyi</i>).....	42.8	66.6
<i>Vitis cinerea</i>	78.5	23.8
<i>Rhus lanceolata</i>	92.8	9.5
<i>Yucca rupicola</i>	64.2	28.5
<i>Cercis reniformis</i>	78.5	0.0
<i>Smilax bona-nox</i>	35.7	28.5
<i>Mimosa borealis</i>	47.1	23.8
<i>Bumelia</i> sp.....	35.7	23.8
<i>Chilopsis linearis</i>	57.1	4.7
<i>Rhus toxicodendron</i>	50.0	9.5
<i>Opuntia</i> sp.....	42.8	4.7
<i>Quercus breviloba</i>	7.1	14.2
<i>Forestiera</i> sp.....	7.1	14.2
<i>Rhus trilobata</i>	14.2	9.5
<i>Amorpha</i> sp.....	14.2	9.5
<i>Ungnadia speciosa</i>	21.4	0.0
<i>Garrya lindheimeri</i>	14.2	0.0
<i>Ulmus crassifolia</i>	0.0	9.5
<i>Lantana horrida</i>	14.2	0.0
<i>Cissus</i> sp.....	7.1	0.0
<i>Melia azedarach</i>	7.1	0.0
<i>Coccolus carolinus</i>	7.1	0.0
<i>Ptelea trifoliata</i>	0.0	4.7
<i>Lonicera</i> sp.....	7.1	0.0
<i>Celtis</i> sp.....	7.1	0.0
<i>Nolina</i> sp.....	7.1	0.0
<i>Prunus</i> sp.....	7.1	0.0

rats, a total of 33 species grew (average number of species per quadrat, 8.8; maximum, 19; minimum, 3). In two quadrats on an ungrazed burn area (not burned recently) the average number was 6.9 (maximum, 13; minimum, 3). In one quadrat in Mexico (Sierra Padilla), 14 species of woody plants were found. In the Texas quadrats in which only two or three species of woody plants were found, the cover was provided by cedar with evergreen sumac understory, live oak with cedar understory, or live oak with evergreen sumac understory. In the two Oklahoma quadrats in which only four species of woody plants were found, the cover was provided by blackjack oak and cedar, and blackjack oak, post oak, and cedar.

One other feature of the vegetation was considered—the age of the trees. As Beecher (1942) has pointed out, an animal population can be no more stable than the plant community in which it lives. In the case of the black-capped vireo, the habitat must remain suitable for a certain minimum of time, just as there must be a certain minimal area of suitable habitat for a population to establish and maintain itself.

In the Oklahoma study area, red cedars 9-10 feet high and with basal diameters of 2 to 3 inches were

estimated, by counting growth rings, to be 18 to 19 years old. Oaks of this size were found to be 12 to 38 years old. A buckeye shrub (*Aesculus glabra*) 6 feet high with basal diameter of 2 inches was estimated to be 13 years old. Sumac (*Rhus glabra*) 5 feet high, with basal diameter of $\frac{5}{8}$ inch was 5 to 6 years old, this plant having grown since the last burn in the area seven years previously. Two oaks (*Q. undulata*) from Sierra Madera with basal diameters of one inch had 19 growth rings. On burns within the main part of the vireo's range (Texas and Oklahoma), shrub growth can attain a height of two to three feet in three years (if conditions are usual). From this state, growth is slow, probably because of the shallowness of the soil which limits the moisture available to plants. Black-capped vireos are most often found on steep slopes, simply because the woody growth remains a suitable size for longer periods than it does in areas where there is more soil. Rugged terrain provides many micro-climates and varied edaphic conditions so that the vegetation grows irregularly, forming clumps. Flat land tends to grow forest or prairie depending on climate and soil. Only in a very limited area (prairie-forest ecotone) can vacillations in climate produce dwarf forests on flat land, and such shinnery, because of the evenness of its height and arrangement, is not attractive to black-capped vireos. Instead the bird seeks ravines which can provide the conditions mentioned above.

The vegetation must be distributed over certain area (a spatial requirement), not arranged linearly in rows or strips as with roadside shrubbery. The black-capped vireo sometimes nests on the roadside, but only when a suitable area adjoins the roadside. The species does not utilize roadside edge as does the Bell's vireo.

VEGETATION OF THE WINTERING AREA

The wintering habitat is difficult to describe. The requirements of the species apparently are less strict in the non-breeding season than in the breeding, and so there is a wider range of vegetational types in the winter habitat than in the summer. In southern Sinaloa (near Concordia, which lies just east of Mazatlan, in the first foothills of the Sierra Madre Occidental), the winter habitat was arid scrub 2-10 feet in height (Fig. 5). Prominent among many woody species were *Ardesia revoluta*, *Bursera* sp., *Mimosa* sp., and *Ipomoea intrapilosa*. Large cacti (columnar cereus) were interspersed throughout the woodland. When I was there (December) few of the trees had leaves, though some were flowering, especially *Ipomoea*. The aspect was not unlike the breeding habitat in Texas at about arrival time.

In Nayarit, near Las Varas on the coast west of Compostela (Fig. 6), the winter habitat was more mesic and luxuriant than that of Sinaloa. Here the bird chose cut-over and secondary growths that were composed of an incredible mixture of woody plants, palmettos, palms, cacti of various types, and mimosa. Especially prevalent were *Combretum farinosum*, and the large leaved shrub, *Bixa orellana*. Thickets of



FIG. 5. Arid shrub, wintering habitat in Sinaloa, Mexico. Much of the vegetation is without leaves as it is the dry season of the year. Photo taken December, 1955, three miles west of Concordia.

the latter appeared to be especially favored by the black-capped vireos. This habitat seemed different (except for its shrubby nature) from any in which I had found the vireo, and I suspect it is a secondary habitat which has become available only in the wake of cutting and clearing.



FIG. 6. Cut over forest, wintering habitat in Nayarit, Mexico. Photo taken in December, 1955, of hilly terrain 20 miles west of Compostela.

CLIMATIC ASPECTS

Climatographic studies of the breeding area should provide indices of conditions most suitable directly and indirectly to the species. Climatographs were prepared using data supplied by the United States and Mexican Weather Bureaus (1956 Climatological Data for U. S., and Atlas Climatológico de Mexico 1939). Long term monthly means for April, May, June, July, and August were plotted on the graphs as April 4, June 6, etc. Climatographs were prepared for the wintering area also, using monthly means (the average of 14 years, 1921-1935) for September through March, numbering the months on these maps as September 9, October 10, etc.

In Fig. 7, Climatograph A, lying within B, represents data for Kerrville, Texas. This locality was considered most representative of the black-capped vireo's habitat because the bird has long occupied it continuously and successfully, it lies in the central

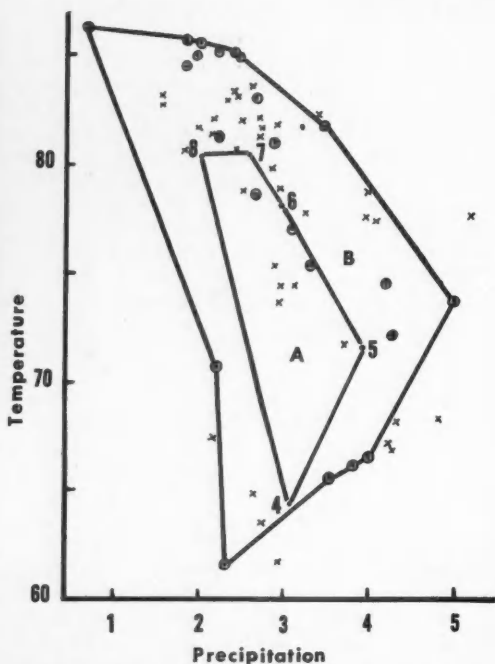


FIG. 7. Monthly means of temperature (in degrees Fahrenheit) and precipitation (in inches) in breeding area. Enclosure A represents Kerrville, Texas; enclosure B, other localities in which the black-capped vireo breeds, with points marked as O. Points marked as X are from localities formerly occupied. Numerals represent months (4 is April; 5, May, etc.).

portion of the breeding range, and its weather data appears to be close to the mean of all areas in which the bird breeds. Climatograph B, which encircles A, is based on data from weather stations near localities now occupied by the vireo: Anadarko, Oklahoma; Boerne, Uvalde, Dallas, Waco, and Austin, Texas. Encircled points are from these localities. Other points are from localities in which the vireo has been known to occur (and breed): Cimarron, Jetmore, Medicine Lodge, and Winfield, Kansas; Apache, Tulsa, and Oklahoma City, Oklahoma; and Junction and San Angelo, Texas. April temperatures were omitted for Jetmore, Cimarron, Medicine Lodge, and Winfield, Kansas, and for Tulsa and Oklahoma City, Oklahoma as the bird does not arrive until late April in these places. Climatograph B, therefore, represents the limits of rainfall and temperature in localities in which the vireo regularly breeds. Points outside of B are from localities occupied sporadically by the black-capped vireo.

Fig. 8 depicts rainfall and temperature at Kerrville, Texas, and at several localities just west of the western limits of the breeding area. The Davis Mountains in Jeff Davis County, Texas, and the Glass Mountains near Alpine, in northern Brewster County, Texas, have shrubby habitat which appeared

to be suitable for breeding, but I saw no birds there in 1955 and 1956. Figure 8 suggests that western limits of breeding may be determined in part by coolness. This picture is based on long term means. In some periods the climate may allow the vireo to become established, in others it is unfavorable.

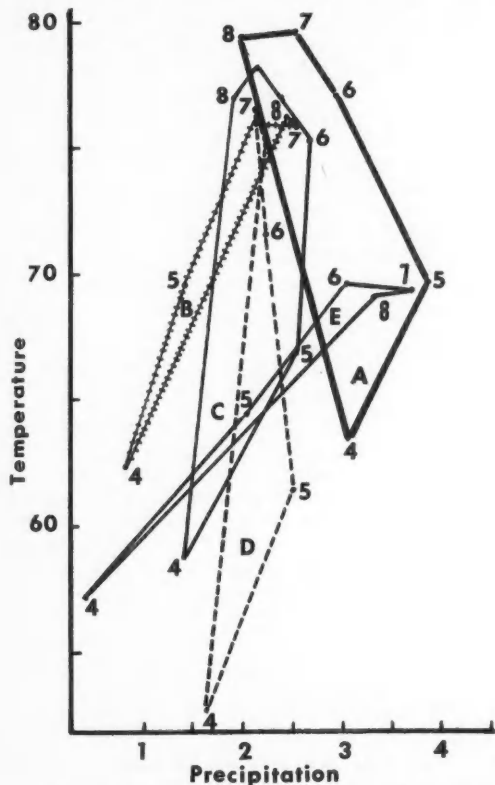


FIG. 8. Monthly means of temperature (in degrees F.) and precipitation (in inches) in localities west of breeding area. Enclosure A represents Kerrville, Texas; B, Alpine, Texas; C, Lubbock, Texas; D, Boise City, Oklahoma; and E, Mount Locke, Davis Mts., Texas. Numerals represent months (4 is April).

Fig. 9 compares precipitation and temperature of three localities to the north and east of the bird's range with that at Kerrville. Lack of suitable habitat, rather than climate, limits the vireo in this direction. Greater amount of precipitation indirectly affects the distribution because the vegetation grows rapidly and soon becomes too large to provide acceptable habitat.

At present, drought conditions have brought about a reduction in the breeding range, especially in the north and west. In 1885-1900, the vireo bred in southern Kansas and western Texas (San Angelo). Kincer has depicted a gradual decrease in precipitation and an increase in temperatures since 1910 (Tannehill 1947). Between 1850 and 1910 rainfall was greater and temperatures cooler (Bowman 1935).

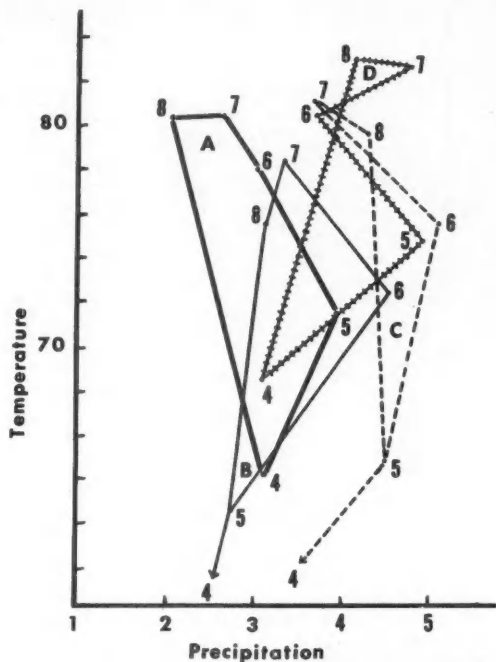


FIG. 9. Monthly means of temperature (in degrees F.) and precipitation (in inches) in localities north and east of breeding area. A represents Kerrville, Texas; B, Omaha, Nebraska; C, Manhattan, Kansas; D, Houston, Texas. Numerals represent months.

Though the vireo occupies a zone of transition between humid and dry climates, a zone in which fluctuation is characteristic (Kendall 1935), long term trends toward aridity may have a pronounced effect on its distribution.

Fig. 10 depicts September-to-March temperature and precipitation on the wintering grounds. Line C represents conditions (monthly means numbered) at San Blas, Nayarit, Mexico, a locality having intermediate position and climate. Enclosure A represents the range of conditions from Ciudad Obregon, Sonora, to Acapulco, Guerrero, Mexico, and from sea level to 3011 feet (Tepic, Nayarit). Enclosure B (Fig 7) represents the range of conditions on the breeding grounds in Texas and Oklahoma from April to September. Line D indicates the limits of most of the localities of the wintering grounds (the larger enclosure included Ciudad Obregon, Sonora). Localities included in preparing A are: Ciudad Obregon, Sonora; Moreorito, Culiacan, and Mazatlan, Sinaloa; Acaponeta, Tepic, and San Blas, Nayarit; Manzanillo, Colima; and Acapulco, Guerrero.

During most of the winter the wintering grounds are much more arid than the breeding grounds. Only in September and October is there as much or more rainfall than in the breeding area. This aridity can be endured because it follows a rainy season, thus being quite different than if it were a drought or des-

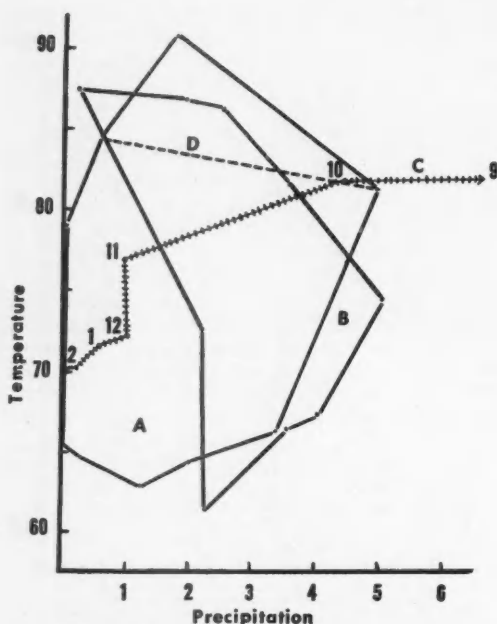


FIG. 10. Monthly means of temperature (in degrees F.) and precipitation (in inches) in wintering (enclosure A) and breeding areas (enclosure B). Line C represents San Blas, Nayarit. Numerals represent months (10 is October; 11, November, etc.).

ert condition. Monthly means of rainfall in the area utilized by the bird vary from 0.0 to 6 (possibly 10) inches. Moisture is frequently provided in the form of fog along the coastal lowlands of Mexico.

The temperature limits of the breeding and wintering grounds are about the same, monthly means falling between 60° and 87° F. When I was in Mexico in late December, 1956, I recorded maximum daily temperatures of 85-98° F near Concordia, Sinaloa, and at 86° F at Las Varas, Nayarit. Minimums were 58-62° F near Concordia, and 51-54° F at Las Varas. These recordings were taken in the field at the places I saw black-capped vireos wintering. The U. S. Weather Bureau provided the following data:

Locality	Winter Temperature	
	Extreme Highest	Extreme Lowest
Acapulco	97 (Oct.)	60 (Feb.)
Campeche	95 (Mar.)	54 (Feb.)
Mazatlan	92.1 (Sept.)	52.2 (Jan., Feb.)
Culiacan	104 (Sept.)	38 (Jan.)

The northern limits of the wintering grounds are probably set by low extremes of temperature. The bird appears to prefer temperatures well above freezing, though it can withstand brief cold spells. It is relatively heat tolerant.

The wintering and breeding grounds do not have greatly differing climates. The more variable factor,

rainfall, has broader limits in the winter. The black-capped vireo has a narrow range of climatic tolerance, and its distribution is relatively limited, suggesting that it does not adapt readily to new environment.

I have witnessed hailstorms, rainstorms, dust storms, and high winds while observing the black-capped vireos, but have never seen any losses of eggs, young, or adults because of unusual weather. Bunker (1910) reports loss of eggs from nests following a severe storm.

LIFE HISTORY

An intensive study of the life history of the species was made to find factors which might account for its limited numbers. Since so little is known of this species, many of the observations made are presented in this paper.

ARRIVAL

The black-capped vireo regularly arrives about a week after the average date of the last frost in the breeding areas. Table 3 lists arrival dates in various localities. Males regularly arrive a week or two in advance of the females.

TABLE 3. Arrival Dates of Black-Capped Vireo at Selected Localities in Breeding Range.

Locality	Date	Observer
Bandera County, Texas.....	March 19	Ragsdale (Cooke 1888)
Kendall County, Texas.....	March 27	Brown (1882)
Kerr County, Texas.....	March 19	Lacey (1911)
	(earliest)	
	March 24	
	(average)	
Comal County, Texas.....	March 24	Graber (1955)
	(males)	
	April 7	
	(females)	
Travis County, Texas.....	March 13	Shipwash (Kincaid 1954)
	(earliest)	
	Late March	Simmons (1925)
Dallas County, Texas.....	April 1	Kelley (1935)
	April 9	Stillwell (1939)
	(earliest)	
Cooke County, Texas.....	April 17	Ragsdale (op. cit.)
Caddo County, Oklahoma.....	April 25	Graber (1954)
	(males)	
	April 17	Graber (1955)
	(males)	
	April 30	
	(females)	
Comanche County, Kansas.....	Late April	Goss (1885)

TERRITORIES

On arrival the male chooses a territory which remains his as long as he defends it. Observations of banded birds for a period of three years on a study tract in Caddo County, Oklahoma, indicate that male black-capped vireos are attached to their territories and are not likely to move far from them.

Nine of twelve males banded in 1954 returned in 1955. Of these, four occupied identical territories for the two seasons, and five occupied territories adjoining those of the first season. One of the latter

changed territories in mid-season. In 1956, I found five males that had returned to the area for the third year. Three of these maintained the same territories all three seasons, and two occupied the same territories for the last two seasons. Both of the latter had moved to adjoining territories after the first season. Four males banded in 1955 returned in 1956. Of these, three remained on the same territories they had had before, and one moved nearly half a mile, though his mate of the former season remained on their former territory. Both the bird which moved and his former mate had new mates.

Five of twelve females banded in 1954 returned in 1955. One remained on the same territory, two were on territories adjoining their former territories, and two had moved about a quarter of a mile. In 1956, I found two of the females banded in 1954. One may have occupied the same territory all three summers, though I did not see her in 1955. The other had moved to a territory adjoining her 1955 territory which in turn had adjoined her 1954 territory. Thus she had occupied three adjoining, though separate, territories in three seasons. Two females banded in 1955 returned in 1956 and each occupied the territory it had had the previous season.

The territory includes the space in which the pairs engage in all their daily activities, though in some instances they leave their territories to reach watering areas shared by all. The boundaries of territories studied changed but little in three years of observation. If a territory is unoccupied, neighboring birds tend to occupy it, thus enlarging their own territories. The male that changed territories in mid-season was in poor condition as the result of a foot infection. There were a few unmated males in marginal areas that moved in to gain a mate or a more desirable territory whenever chance allowed.

Territorial limits were determined by watching banded birds throughout the season and by "driving" them. I drove the males slowly to points at which they would go no farther but turned back. In some cases the neighboring male came to that place and announced his boundary. I measured some of the territories with which I was most familiar and found that they ranged from 2.5 to 4.6 acres (average 3.7). These measurements are only approximate because of the roughness of the terrain. Territories in other localities in similar habitat (oak-cedar scrub) appeared to be about the same size. Territories in burnt-over, mixed-deciduous scrub seemed to be slightly larger. Brewer (1955) gives the size of a white-eyed vireo (*Vireo griseus*) territory in Illinois as 0.33 acres. Hensley (1950) found the territory of a pair of Bell's vireos (*Vireo bellii*) in Illinois to be 3.1 acres in size.

Territories in the Caddo County study area form a mosaic about the canyon heads, and this, I am convinced, is because the tree growth in such places is of the proper size and kind. Bunker (1910) expresses this same idea, namely, that the bird chooses not the lay of the land, but the vegetation.

Males maintain territory by song. There is a

special territorial song—a rapid, bubbling song, much like (if not the same as) the courtship song but usually louder. I have never seen any more violent action between males than that of one male flying (pouncing) at another.

PAIR FORMATION AND COURTSHIP

Pairs were formed immediately upon arrival of the females. The female appeared to choose the male and territory together, mating with a male on or near the area to which she became attached. Pairs appeared rather stable. Changes occurred when one of the pair failed to return to breeding grounds after winter, when one or the other was incapacitated by an accident, or when a male was occupied with caring for the first brood and a nearby male was available for starting the second brood.

Twelve pairs were banded in 1954. The only female that I know to have been double-brooded changed mates between broods. In 14 re-nesting attempts involving six pairs, only one pair changed mates, this exchange involving the double-brooded pair. I know of two pairs that were double-brooded in 1955, and both remained mated for the second brood. In seven re-nesting efforts, involving six pairs, only one pair changed mates. I believe that pairs remain mated throughout a season because re-nesting and starting of second broods begin at different times, and therefore only the two birds involved are likely to be at the same stage in the reproductive cycle. The members of only two pairs survived three seasons. One pair I know were mated in 1954 and 1956, and probably in 1955, though I did not see the female that year. The other two remained mated for two seasons, through a total of at least three nestings, but separated the third season. Two pairs returned in 1956 for their second season, and one remained mated; the other changed mates.

Courtship consists of song and display. There is a special courtship song which is made up of a series of low, rapid, bubbling notes, entirely lacking the characteristic phrasing of the regular song. The male follows the female about the territory singing to her.

In one courtship flight I witnessed, the male flew in a downward arc from a perch 30 feet high to a perch three feet high, fluttering his wings and displaying his back while singing the courtship song before the female who was perched near the point of his departure. She then flew to where he alighted. In another instance, the male fed a juvenile of the pair's first brood, then left his perch in pursuit of the female. Both birds gyrated about the sky some 40 feet up, the male following the female closely, but never quite catching her. Chipping sounds ("tup, tup, tup") were given during the flight, then the male alighted and sang a courtship song.

One display which immediately preceded copulation consisted of several short fluttering flights about a foot about the perched female, while singing the courtship song. These flights may have been attempts to mount the female. The two times I watched copu-

lation, the female was perched about eight feet up in a tree. The male hovered over her, then settled lightly on her back for a moment. Copulation took place in mid-morning both times.

THE NEST, ITS SITE AND CONSTRUCTION

The male covers his territory thoroughly before the arrival of the female, and while doing so he looks for nest sites. In fact, I have seen a male build the rim of a nest during this time. I have watched males go to a likely-looking crotch and examine it carefully, even circumscribing an arc with the head between the branches as if weaving fibers.

When the female arrives, the pair wanders about the territory looking at nest sites together. I suspect that the female makes the choice, for I saw a pair examine a crotch to which the male had already attached a few wisps of spiderweb, but they began building the next day at another site. Furthermore, one female built a nest for a second brood largely if not entirely by herself while the male cared for the first brood. I know, also, of two unmated males that selected typical nest sites and built the rims of nests but never finished them. One of these built two nest rims during the summer. The completion of a nest appears to require the attention and efforts of the female.

The nest is generally placed almost as far out on the branch as it is about the ground. The height of all 67 Oklahoma nests ranged from 18 to 66 (average, 34.5) inches. That of all 34 Texas nests in 1956 ranged from 27 to 74 inches (average, 44.0). Simmons (1925) gave nesting heights in Texas as two to six feet, rarely 15, usually four. Five nests in central Coahuila, Mexico, were one to two feet above the ground. Nests placed in Spanish oaks in Texas had an average height of 59.6 inches. The deer browse line of these trees was just a little under five feet. Nests in the same area in cedars, which are never browsed, had an average height of 39.7 inches. The size of the tree or shrub probably also affects the location of the nest.

In 70 Oklahoma nests examined, 51 were placed in blackjack oak (*Quercus marilandica*), 12 in post oak (*Q. stellata*), 3 in chinquapin oak (*Q. muhlenbergii*), 2 in buckeye (*Aesculus glabra*), 1 in redbud (*Ceris canadensis*), and 1 in poison ivy (*Rhus toxicodendron*). I found one old nest in a red cedar (*Juniperus virginiana*) which I am certain was that of a black-capped vireo.

In 37 Texas nests, 12 were found in Spanish oaks (*Q. texana*), 11 in evergreen sumac (*R. virens*), 9 in mountain cedar (*Juniperus ashei*), 3 in sumac (*R. lanceolata*), 1 in live oak (*Q. virginiana*), and 1 in white oak shinners (*Q. brevifolia*).

Of five nests found in central Coahuila, Mexico, four were in scrubby oak (*Quercus* sp.), one in madroño (*Arbutus texana*). Nests have been found also in elm (probably *Ulmus americana*) (Goss 1885); dogwood, wild plum, chinaberry (Bunker 1910); mesquite (Davie 1898); and elm (probably cedar elm,

Ulmus crassifolia) (Simmons 1925). An unusual nest site in a pine was described by Singley (1887).

Certain nest sites were used repeatedly by black-capped vireos, for I have found an old nest of the previous season on the ground beneath occupied nests on several occasions. I have observed males burst into courtship song as they hopped about old nests. One unmated male regularly visited an old nest and sang courtship songs in the tree above it. Finally the old nest fell, and he built a nest rim in the same crotch. Two sites were used for at least three years in succession. While the sight of an old nest definitely stimulates the birds, the location itself may be attractive. In 1954 I removed a nest and its crotch; the following year a different pair of vireos built in the same tree in a crotch near the site of the 1954 nest.

Bunker (1910) suggested that the nest of the black-capped vireo is placed in the center of a clump of bushes, while that of Bell's vireo is placed at the edge. In 31 of 70 Oklahoma nests, and 25 of 38 Texas nests, the nest was placed in the center. In the remaining 52 nests (13 Texas, 39 Oklahoma) the nest was placed at the edge. I have seen a number of Bell's vireo nests that were in the center.

The nest is a cupped, pensile structure, typically vireonine. Brewster (1879), Goss (1885), Davie (1898), Bunker (1910), Simmons (1925), and Morse (1927) gave descriptions of nests. Fig. 11 shows an adult male at a nest. Average measurements in centimeters of 45 Oklahoma nests are: outside depth, 5.8-6.2; largest outside diameter at rim, 5.5-5.9; greatest thickness of wall at rim, 0.9-1.1; and inside depth from rim to bottom, 3.7-3.9.

The materials used in construction of nests were dead leaves, dried grasses, plant fibers, cottony plant substances, cedar bark, paper, wool, and spider-web



FIG. 11. Adult male black-capped vireo at nest in *Rhus virens*. Photo taken July, 1956, at El Rancho Cima, Comal County, Texas.

or similar substances (caterpillar silk). The chief construction materials in nests built on oak-cedar habitat were cedar bark and oak leaves which were bound together with spider-web. In areas where there were no cedars, grass and grapevine bark were used instead of cedar bark. In Mexico, the dried, paper-like leaves of yucca were used. Thus the structure of the nest reflects the nature of the habitat. Bits of paper, spider cocoons, or other white, tissue-thin materials are often placed decoratively on the outside of nests. The sparse lining is of fine grass stems and panicles.

The materials for the nest are for the most part gathered nearby. I have watched both members of pairs go to cedars close to nests they were building and pull small strips of bark from the lower, almost horizontal branches. One female flew down and picked up a dead leaf from the ground not ten feet from the nest site. I have seen a male tugging at leaves on a dead branch of an oak about three feet above the ground for a nest that he was starting about 10 or 15 feet away. A pair in Texas stripped bark from a mustang grape about ten feet from their nest site. One male on my study area in Oklahoma carried a piece of tissue paper up into a cedar. There he tore off small pieces and carried them to the nest about thirty feet away. Females often gathered spider-web from the topmost branches of dead oaks which were close to their nests.

The length of time required for completion of the nest varies with the pair and the season. First or early summer nests are usually completed in four or five days. Later nests are usually built more rapidly. In one case, the total time lapse between the loss of hatchlings and the laying of the first egg in a subsequent nest was five days. The longest time observed between the beginning of building and the laying of the first egg was 16 days. The period between the completion of the nest and laying of the first egg is usually a day.

Although both sexes work at building the nest, the female accomplishes more since the male pauses to sing and defend his territory. Bunker (1910) said that the male did not assist in building. Some males appear to be rather inefficient at building. I observed one whose contribution toward building was to bring a bit of material to the partly finished cup and just drop it in. Some females carry great mouthfuls of many pieces of material to their nests.

I observed one pair from 12:00 noon to 1:00 p.m. working on a half-built nest and found that they made 22 trips with nest material. The male made eight trips, the female 14. The male came and sat on the nest twice without bringing material, the female did this once. The male sang short snatches of song as he worked. Sometimes he merely accompanied the female as she got material and brought it to the nest. I never saw him work at weaving with his bill as did the female. He limited his building to sitting in the nest and turning about, fitting it to his body.

Bunker (1910) described the beginning of the

building of a nest. He said the female attached fibers to the twigs making a fringe, then it flew down, caught up a fiber in its bill, and flew to the opposite side of the crotch to attach it. I have never observed this stage of nest building, for if I remained in the vicinity of a barely-started nest, the birds invariably deserted. Most of the nests I watched were already a shallow platform of fibers, and as material was added the birds sat on the nest, shaping it and making it deeper by stretching the loosely connected network. After a slow start (in terms of the amount of structure made), the birds build rapidly for a day or two, adding the bulk of the nest, then adding the lining slowly. Nests are never re-used; a new nest is built for each clutch. Four nests are the most I have seen any one pair build in a season.

LAYING, THE CLUTCH, AND INCUBATION

Egg laying reaches a peak (in number of eggs laid in nests under observation) during June in Oklahoma, and during May in Texas. I found eggs hatching as early as April 23 in Hays County, Texas. In Caddo County, Oklahoma, the first eggs were laid in late April and early May.

I made an effort to determine the time of laying for four different females, and found that they laid at about 6:00 a.m. in June in central Oklahoma. In each case, the daily procedure during egg-laying was much the same. The singing of the male, at about 5:00 a.m., was the first evidence of activity of the pair. The male came toward the nest, but never went down to it. The female came to the nest a little later (10 to 20 minutes before laying) and got on it. In laying, the female, having been sitting rather deep in the nest, rose up, arched her tail downward, pushed her vent toward the bottom of the nest, while her foreparts rose out of the nest, and appeared puffed out. After a few seconds, she settled again. Upon flushing her, I found the new egg not yet dry. If left undisturbed, she continued to sit on the nest for 20 to 40 minutes before leaving.

I watched one female lay three eggs, finding that she laid egg #1 at 5:57 a.m., egg #2 at 6:05-08 a.m., and egg #3 after 6:14 a.m. (the male was on the nest until then). In every case I have observed, laying has occurred on consecutive days.

Both birds sit on the nest during at least part of the day on which the first egg is laid. I watched one nest from 5:30 to 10:35 a.m. The female got on the nest at 5:45, laid at 5:57, and remained until 6:30. After a brief absence she returned to sit on the nest for a total of one hour and 46 minutes (intervals of 31, 12, 33, 15, and 15 minutes); the male was on for one hour and 27 minutes (intervals of 1, 31, 18, and 37 minutes); and the nest was unattended for two periods (19 and 17 minutes). I have seen other black-capped vireos on their nests after the laying of the first eggs, but they did not spend the night on the nest until the second or third egg had been laid. I think the habit of daytime covering of the eggs as soon as they are laid has survival

value for the black-capped vireo in that in this manner they are safeguarded to some extent from cowbirds (*Molothrus ater*).

Four eggs usually comprise a clutch. In 45 nests, there were four eggs; in 26, there were three. However, in some nests holding three eggs, four eggs may have been laid, one having been removed before I checked the nest. I found no indication that clutch size in the north was larger than that in the south. I have never found a nest with more than four eggs. If an egg is removed during laying, the clutch may be completed, but there will be no more than three eggs in the nest. If more than one egg is removed, usually the nest is deserted, unless cowbird eggs replace the loss. I have records of seven second nests containing four eggs, and of only one containing three. In one case, both the first and second clutches consisted of three eggs. In 1954 in four nestings one female laid clutches of four, two (interrupted by cowbird), two (interrupted), and three eggs (total: 11 eggs). In 1955 she laid three four-egg clutches.

I have seen a total of 285 eggs in 83 nests from northern Oklahoma to central Coahuila, Mexico, and all have been immaculate white. The egg is similar to that of the Bell's vireo, but more pyriform. Bent gives the average measurements for 50 black-capped vireo eggs. I have measured only six eggs and they fell within these measurements except for one which measured 17.2×11.8 mm.

The average weight of 21 one-day-old eggs from six different females was 1.59 grams. The eggs lost weight throughout incubation so that by hatching time they weighed only 1.1 to 1.3 grams. This gradual weight-loss was about the same from day to day in artificially incubated eggs. It was irregular in the nests, suggesting that the habits of the birds and the weather may have affected it.

In an attempt to determine ecological differences between black-capped & Bell's vireos, I exchanged eggs between two nests of these species. A Bell's vireo egg lost more weight during incubation in a black-capped vireo nest than did three black-capped vireo eggs in the same nest, but lost less weight than did three other eggs of the same clutch in the parent Bell's vireo nest. A black-capped vireo egg lost less weight during incubation than did three Bell's vireo eggs in a Bell's vireo nest, but lost more weight than did three other eggs of the same clutch in the parent black-capped vireo nest. This difference may have lain in incubation habits, in nest situation and in the eggs (possibly the porosity of the shell). Both transposed eggs hatched and the young were reared by the foster parents.

Incubation begins with the laying of the second or third egg. One female started incubation with the second egg of a four-egg clutch, another with the third egg of a three-egg clutch. Both of these were re-nestings. From the sequence of hatching, it appears that incubation often starts with the second egg. I have counted incubation as starting on the

day preceding the first night the bird spent on the nest.

Both sexes incubate. The female develops a large brood patch which the male lacks. I watched one nest for 15 hours continuously on the first day after the clutch was completed (on the fourth day of incubation), and again on the 14th day of incubation (two days before hatching), to see what occurred during both the early and late stages of incubation. On both days, incubation was shared by the male and female, but since the female spent the nights on the nest, she actually accomplished about two-thirds of the incubation. Table 4 summarizes the data obtained on attentiveness.

TABLE 4. Observations of a Nest During Incubation.

	BIRD ON NEST		Nest unattended
	Male	Female	
Total time in minutes on 4th day of incubation.....	411	386	103
Total time on 14th day.....	376	458	51
Number of periods on 4th day of incubation.....	10	15	11
Number of periods on 14th day.....	17	20	18
Average time for a period on 4th day of incubation.....	41	26	9
Average time for a period on 14th day.....	21	23	3

On the fourth day of incubation, the longest inattentive period occurred in mid-day (11:16-11:30 a.m.) and was 14 minutes in duration. Attentive periods ran about 20-40 minutes in the morning and were longer in the afternoon. During the cooler parts of the day, the birds sat deep in the nest, but in the heat of the day they sat high, apparently thus regulating the temperature of the nest contents.

On the 14th day of incubation, the longest inattentive period was 10 minutes. Attentive periods were shorter than on the fourth day but total attentiveness was slightly more. The nest was left unattended for 5.7% of the time observed as compared with 11.4% on the fourth day. Part of this difference may be accounted for by assuming that the birds were more disturbed by my activities and by the blind at first than they were later.

At this nest and at others that I have observed, there was a definite pattern of behavior during the changeover of birds at the nest. Usually the male sang a phrase or two of the "nest song" as he approached and the female replied with a soft "shrad" and left the nest. The male settled on the nest. On returning the female again gave a soft "shrad" and the male left, singing a phrase or so as he went. Once in a while he sang just before leaving, but such songs certainly can not be compared with those given by warbling vireos (*Vireo gilvus*) on their nests. One female that I watched tending a brood alone (the male was caring for the first brood), announced her approach to the nest by an unmusical phrase or two. While she was incubating, the male often came to the tree with the first brood and called her off the nest and she left and returned with a soft "shrad."

Both birds roll the eggs from time to time with their bills while sitting or just before settling on them.

The male apparently does not incubate eggs of the second brood, being occupied with the care of the first brood. In one case in which I have data on the second brood of a banded pair, the female took another mate to help her with the second brood; in another case the female accomplished the task by herself. I have observed other females (unbanded) carrying out incubation by themselves while what I took to be their mates cared for young probably of the first brood. The female that incubated the eggs of the second brood alone left the nest unattended 18.8% of the time that I watched it. She guarded the nest closely, never leaving its vicinity. If I could not see her and put my head out of the blind, she immediately scolded.

The total incubation period varies from 14 to 17 days. I determined the incubation period 13 times in Oklahoma and twice with artificial incubation. The longer periods occurred early in the season, and when nests were cowbird parasitized. Most of the variation probably can be explained by variation in the attentiveness of the parent birds. Some may be due to climatic influences. Attentiveness is lessened when a cowbird egg hatches, but this is not always the case. In two nests with cowbird chicks the vireo eggs hatched in 14 days.

HATCHING, THE CHICK, AND PARENTAL CARE OF YOUNG BIRDS

The eggs usually hatch over a two-day period, further indication that incubation is started before the clutch is complete. In seven nests the second and third eggs hatched on the same day; in three nests, they hatched on different days. In one nest, all eggs (four) hatched on the same day. Hatching occurred at any time of day, and probably of night. I have seen eggs remain pipped for as long as 12 hours before hatching. The egg is pipped around its greatest circumference and the chick pushes and kicks out.

Eggshells are promptly removed from the nest. At one nest, they were carried away within 15 minutes after hatching. At another nest I watched the female remove them. She probed into the nest while perched on the rim, and finally lifted the shell up over the rim. Both halves fell to the ground, and she flew down and scouped up one half and carried it off in her bill. The other half remained where it had fallen. Once, I found a marked half-shell about 75 yards from the nest in which the egg had hatched that morning. It was lying near the edge of the water where the vireos drank. Several times I have found pipped eggs on the ground near the nest. I have never seen the birds eat any shells.

At hatching, the chick is naked and blind, and weighs about a gram. The skin is yellowish pink, as are the bill and feet. The gape is yellow and has an upward angle toward the eye.

The young gain approximately a gram per day

until they weigh between seven and eight grams. Their weight upon leaving the nest is about eight grams. Fig. 12 shows growth curves for chicks in one nest, and a theoretical curve based on exactly 1 gram per day increase in body weight. I stopped weighing the chicks when they were six and seven days old because handling might induce them to fledge prematurely. Two black-capped vireo fledglings out of the nest for one day and two days weighed 8.1 and 6.88 grams respectively.

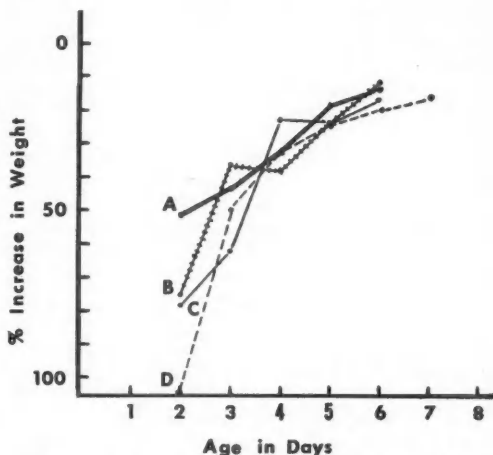


FIG. 12. Growth curves of black-capped vireo brood. A is first chick hatched; B, the second; C, the third. The dotted line D shows a theoretical curve based on 1 gram per day increase in weight.

I observed and compared the development of a black-capped vireo chick hatched from an egg incubated in a Bell's vireo nest and reared in the nest with two Bell's vireo chicks, and of a Bell's vireo chick in a nest with three black-capped vireo chicks. Figs. 13 and 14 show daily weights of the nestlings. I had hoped to repeat this experiment with the white-eyed vireo but was prevented by predation and cowbird parasitism. Both adopted chicks grew fairly well, though the black-capped chick did not do as well as its siblings or its nestmates.

On the day of hatching, tiny blackish feather buds can be seen along the outer edge of the manus and the distal half of the forearm. No other feather buds are visible. By the beginning of the second day a small portion of the mid-dorsal tract shows, but no quills break through the skin until the third day. Feather buds are then visible on the capital and ventral tracts. On the latter they are hard to see because of their light color. On the fourth day the primary buds extend about $\frac{1}{4}$ inch, $\frac{1}{2}$ inch on the fifth day, and about $\frac{3}{4}$ inch on the seventh day. On the eighth day, the feathers unsheath, except for those of the crown. These unsheath on the ninth day. By the tenth day, the young are fairly well feathered, and the primaries are about half unsheathed. On the eleventh day the primaries are about $\frac{3}{4}$ un-

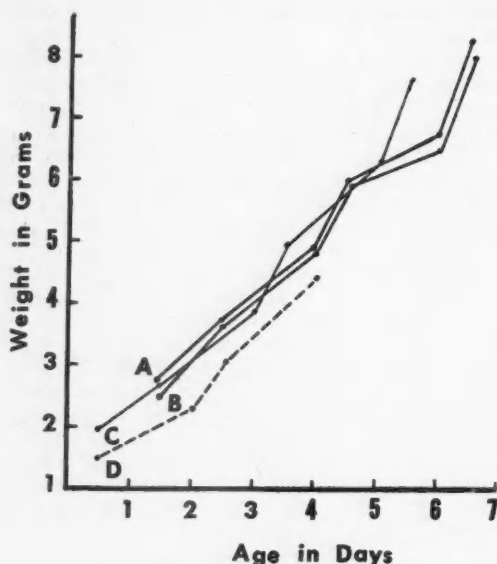


FIG. 13. Daily weights of mixed brood in black-capped vireo nest. A and B are black-capped vireo chicks hatched June 26; C, a black-capped vireo chick hatched June 27; D, a Bell's vireo chick hatched June 28. D fell out of nest and died on fourth day.

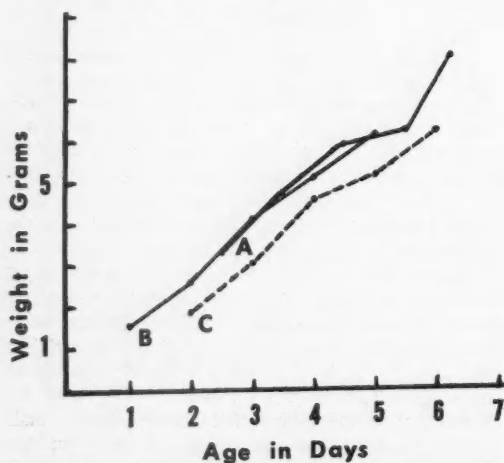


FIG. 14. Daily weights of mixed brood in Bell's vireo nest. A and B are Bell's vireo chicks; C, a black-capped vireo chick. A hatched early June 25; B, on June 26; C, late June 25.

sheathed, and there may still be a few blood quills at the base of the bill.

The young keep their eyes closed most of the time until they are five days old. They grasp the bottom of the nest with their feet and are difficult to dislodge when only a few days old. On the sixth day they first show fear when handled, and are able to sit on a perch. If unduly disturbed they may leave the nest as early as the tenth day. Usually they

leave the nest on the 11th or 12th day. Departure occurred in two nests on the 10th day, in four on the 11th day, in three on the 12th day, and in one on the 13th day. In the last case, the sole juvenile in the nest was retarded in its development, feathering out on the 12th day.

Nest-leaving is staggered. Quite often it begins at sundown. One fledgling hops out of the nest and sits on the branch beside the nest for the night. The following dawn, the remainder leave the nest. The fledglings stay near the nest for a few days. Often they seek shelter in cedars where, were it not for their calls, they would be nearly impossible to locate. They call very frequently for the first day or so, thus maintaining contact with the adults.

As the young become more adept at flying, the family moves about its territory. In the Caddo Co. study area, families moved from the nest-slopes down into the shaded ravine where there was water. I also saw some Texas families move from the hillsides down into more heavily wooded, though dry, stream beds. Generally the family remains on or near its territory until migration, though it sometimes wanders into neighboring territories or even farther.

I watched one fledgling for 44 days after it had left the nest. At noon on the day it left the nest, I found it sitting seven feet up in a cedar about 70 feet from the nest. On the second day it was sitting about 12 feet up in an oak some 120 feet from the nest, and about 50 feet from where it was the day before. It could fly, and I caught it only with some effort. When released, it flew 60 feet. Its landing was awkward.

For the next 25 days, I was able to find the male and the juvenile within 100 yards of the nest. I did not see the female in attendance after the fourth day (June 16). On June 21, I found her with a neighboring male working on a half-finished nest. She had left her first mate who was caring for their single fledgling. On the 43rd day after the young bird had left the nest, the male parent was observed to fly at his offspring in a hostile manner, trying to discourage it from following him and from begging. He even appeared to be trying to escape from it.

The following morning, I found the young bird alone. It was following a small flock of chickadees (*Parus carolinensis*) and gnatcatchers (*Poliophtila cerulea*) about on the territory. It scolded with a high-pitched "shrad," as it had been doing since five days after it left the nest. Then it sang a squeaky song that reminded me somewhat of that of the blue-gray gnatcatcher. I heard the parent male singing in another part of the territory a little later in the morning. He no longer scolded me as he had when attending the juvenile. At 44 days after fledging, this young bird was apparently completely independent of its parents.

I watched the development and postjuvenile molt in a bird that I made captive on the day it left the nest. It took two days for the captive to adjust to captivity, after which it flew toward me begging whenever I entered the room in which it was kept.

For the first few days it called "schrief" every few minutes. Later it called infrequently, presumably only when hungry. At roosting time it gave a "chirrup" note, which it also gave upon awaking, but at no other time. It gave small "kek" notes when a dog entered the room. When it was 24 days old, it gave the typical "schrad" scold note of the adult for the first time.

At 12 days it could preen efficiently. At 15 days it could fly well. On its 17th day it attempted to take food from the forceps with which I fed it instead of merely opening its mouth. Two days later it made its first attempts to find food for itself. It begged "at," then picked up, a larva placed beside it. It made bathing motions for the first time at the age of 24 days. When it was 28 days old, it caught insects and held them with its feet while pecking them apart. It was not very efficient at catching prey, being too slow. At this age it snapped its bill and attempted to bite when handled. At roosting time it flew to me, perching on my head. From the age of 10 days (nest-leaving), it slept in the typical adult position.

The weight of the captive increased gradually from 7 to 9.7 grams, its weight on its 22nd day. The legs had become noticeably blue by its 19th day. The rectrices grew from about 3 mm. at nest-leaving (10 days old) to 28 mm. at 24 days age. When the bird was 32 days old, the sheath-free rectrices were 38 mm. in length.

I noticed the first signs of the postjuvenile molt—two or three greenish feathers in the mid-dorsum—when the bird was 24 days old. At 28 days, the auriculars were molting. At 30 days the molt showed on the nape and occiput, the incoming feathers being darker and about a third longer than those of the juvenile plumage. The greenish first winter plumage formed a V across the back. Bright yellow axillars began to appear. The following day the tips of a few buffy feathers appeared on the breast. At 32 days of age, the lores and eye ring were molting, and the lower half of the back was in first winter plumage.

When the bird was 37 days old, buffy first winter feathers formed an inverted V from the mid-line down the lateral tracts of the breast to the level of the second wingbar. The underlining of the wing had been replaced. The chin was molting. New feathers were coming in on the thighs. The head molt had proceeded from the forehead backward to the level of the eye. The dorsal plumage was about two-thirds replaced, the upper portion still being juvenile. At about this time the molt, which had been progressing rapidly, slowed, probably because of unfavorable environmental conditions. The molt was still not completed, when the bird died accidentally at the age of 50 days. It was found to have been a female.

Within a few hours after hatching, the male begins to bring food for the chick(s). As soon as the male begins feeding, he ceases incubating and brooding. I have never seen any of the males in the nest after all the eggs have hatched, although they did

spend time standing on the nest rim or beside it, guarding and shading the young.

The chicks are brooded by the female during the cooler portions of the day, and at night usually until they are seven days old. During the warmer part of the day, she may sit high upon the nest or stand on the rim. As the chicks grow, the adults spend less time at the nest. At one nest the male spent 327 minutes of his 868 minute day (he was first heard at 5:20 a.m. and last seen at 7:48 p.m.), or approximately 37.6% of his time, standing beside, guarding, or shading the young on the first day after hatching. His longest attentive period was 55 minutes, the shortest two, the average 14. The female spent a total of 179 minutes brooding during day and was on the nest at night (7:10 p.m. to 5:10 a.m.). Her longest daytime brooding period was 62 minutes (6:51 to 7:53 a.m.). After 10:00 a.m., she did not brood again until night. Besides brooding, she spent 160 minutes guarding (longest period 55 minutes; shortest one minute; average 16 minutes). The longest period that the male was absent from the nest was 47 minutes (6:34 to 7:21 p.m.). The female was absent once for 83 minutes (4:38 to 6:00 p.m.).

If the female is at the nest, the male gives the food he brings to her to feed to the young; if she is away, he feeds them. Usually only one item at a time is brought. Males provided roughly three-fourths of the food for the young. On the day of hatching of the last chick at one nest, the male made 77 (79.3%) trips to the nest with food and the female, 20 (20.6%) trips. On the eighth day at this same nest, the male made 73.0% of the trips for food, the female 26.9%. On the tenth day, he brought food 64 (68.8%) times, while the female brought it 29 (31.1%) times. At a nest which held a cowbird chick, the male made 75% of the food-getting trips on the second day, 70.4% on the fourth day, and 65.3% on the fifth day.

Wheelock (1905) mentions regurgitative feeding in vireos. This I have never seen in the black-capped vireo. If it occurs at all, it must be unusual. Lawrence (1953) and Stephens (1918) did not witness it in the red-eyed vireo (*Vireo olivaceus*). Nice (1929) once saw a female Bell's vireo swallow food, then pass it to the young four minutes later.

There appeared to be no set rhythm in feeding the young. Some birds fed steadily, others did not. Generally there is a peak in feeding of chicks in early morning and late afternoon, probably a counterbalancing of the effects of night metabolism without food. Before the early and after the late peak the adults must feed themselves for the night. Fig. 15 depicts the feeding of four young in a nest on their first and tenth days. The number of feedings on both days was the same (93), but much larger items were brought to the young on the tenth day. Data from three nests which held two, three, and four chicks respectively, and covered different ages of these chicks from less than 12 hours to 9 days, revealed that the average number of feedings per chick per hour

varied from 0.8 to 2.6. That is, at the peak of feeding during the day, a chick may receive three feedings per hour, and at the low point it may receive less than one feeding per hour. The most rapid feeding rate I observed was at a nest containing a cowbird chick, which was being fed at an average rate of 10.1 feedings per hour on its fourth day, and of 13 feedings per hour on its fifth day. At the end of the fifth day the chick weighed 18.40 grams, just a little less than four vireo chicks of the same age would have weighed. If this feeding rate is divided by four, then it compares with the rate per vireo chick per hour in other nests.

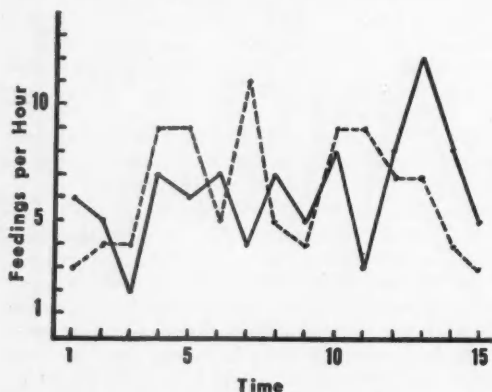


FIG. 15. Feeding rates in a nest with four black-capped vireo chicks. The number 1 (time) represents the first hour of observation, 5:00 to 6:00 a.m.; number 5, the fifth hour, 10:00 to 11:00 a.m., etc. The solid line shows feeding rates on the first day (chicks 12 to 24+ hours old); the dotted line shows the same brood on the tenth day.

During the nestling period the male and female continue to announce their arrival at the nest as they do during incubation. The male nearly always sings a phrase or two of the nest song as he comes to the nest, and the female scolds softly as she arrives and leaves. At first the young respond only to vibration of the nest, but as they grow older, they respond to the signals of the approaching adults. It was hard to ascertain that the chicks responded, but I could see their heads above the nest rim at seven to eight days and they responded at that age. A cowbird chick responded to the sounds of the adult vireos at an age of 5 days.

A vireo, caring for her second brood unaided by the male, was very quiet on the second day after the young hatched, although she scolded softly sometimes as she left or arrived, as she had when incubating. On the sixth day, however, she gave rather squeaky imitations of the male nest song as she arrived. This suggested to me that announcing arrival at the nest is more than a signal between the adults. It appears to be a means of keeping the family together after fledging, and this female seemed to be preparing to assume this task.

After each feeding, the adult bird looks for fecal sacs which appear to be normally discharged only at this time. The nest is kept clean until the chicks leave, at which time the last few droppings may remain about or in the nest. The fecal sacs are usually carried more than 15 feet from the nest before they are dropped. The sacs are eaten by the adults during the first five days of the chicks' lives; from the fifth day on they are carried away. A pair caring for a cowbird chick began carrying away sacs on the second day, but ate about half of them. On the third day they carried them all away. At a nest of four, newly hatched chicks, excreta are removed about once an hour (average rate for entire day), and about a third again as often when they are nine days old. Male and female shared this duty evenly on the first day at one nest. On the eighth and tenth days the male carried away two fecal sacs for every one removed by the female.

The nests are kept clean not only of excreta and egg-shells but also of other debris. This includes dead chicks, if these are small enough for the adult to lift. The disappearance of small vireos in nests with cowbird chicks puzzled me until I observed one nest continuously from the hatching until the chicks were gone. Cowbird eggs are usually deposited in the nest before the vireo clutch is completed. The cowbird egg hatches two to four days before the vireo eggs (12 day incubation period for the cowbird in black-capped vireo nests) and by the time the young vireos hatch, the cowbird outweighs each of them more than ten times. In one nest, a three-day-old cowbird weighed 11.31 grams while its nest mate, a newly hatched vireo, weighed 0.86 grams. The cowbird is able to raise its head up far above the vireo in begging, and gets most of the food. The cowbird requires about as much food as four vireo chicks so it is hungry and begs most of the time. The vireo chick gets scarcely any food, and is trampled and crushed by its parasitic nestmate. After a day or two, the vireo chick dies and its body is removed.

I watched a female vireo remove the bodies of two two-day-old chicks one morning. They had died because of the presence of a cowbird chick. She brought food to the cowbird, then, after feeding it, she began working in the nest. After four minutes she lifted the body of one dead chick out and flew away with it in her bill. She came back, fed the cowbird, and removed the other dead chick. These chicks must have weighed between one and two grams, so she carried between one tenth and one fifth of her own weight.

Stephens (1918) placed certain foreign objects in the nest of a red-eyed vireo and found that the birds removed them. I did not experiment with the black-capped vireo. An incubating female deserted a much-incubated clutch of eggs because a leaf fell in the nest and covered the eggs. In another nest, a young bird died on its ninth day. It was evidently too large to be removed by the adult. The other chicks in the nest fledged as I inspected the dead

nestling. It is well that they did, for a short while later the nest was over-run by ants.

The young are actively defended by the adults who threaten, pounce, and snap their bills at intruders. They also vocally warn the young of danger. I have never observed injury feigning. Hebard (1949) lists no vireos in his catalogue of injury—feigning birds. In general they ignore other species of birds, but I have seen female vireos intimidate female cowbirds by assuming a crouching position and opening the mandibles wide. I once saw a female vireo behave this way toward a field sparrow (*Spizella pusilla*) that happened to startle her on the nest. All adults scolded every time they saw me near their nests, but they were particularly excitable about nest-leaving time.

Two males of double-brooded pairs brought first broods to the vicinity of the nest while the female was incubating the second clutch and caring for the second brood, but I never saw the male or juvenile birds go to the nest. There was no evidence of nest helpers. If the female does not remate for the second brood, she assumes complete responsibility for it up to the time of fledging.

NESTING SUCCESS AND LOSSES

Much of the black-capped vireo's reproductive effort is unsuccessful. From 243 eggs of which I kept record, only 43 chicks that lived to the age of fledging were produced. Thus, 17.6% of the eggs were successful to this degree. Kendeigh (1942) gives data on nesting success for nine species of birds building elevated, cupped nests, and the percentage of eggs that produced fledged young ran from 29 (wood thrush, *Hylocichla mustelina*) to 58 (cardinal, *Richmondia cardinalis*). Nice (1957) reported an average success of 49% (range 38 to 77%) in 24 studies by various investigators as the rate for open nests of passerines in the North Temperate Zone.

I have found only a few nesting success figures for other species of vireos. Lawrence (1953) reported that of 98 eggs in 30 nests of the red-eyed vireo, 59 produced fledged young, a success of 60%. Ely (1957) found that only one of 14 Bell's vireo nests produced young (9.1% of the eggs produced fledglings). Pitelka & Koestner (1942) reported that of 26 nests of the Bell's vireo, five were successful, a success of 19%. Counting any nest successful if it produces one vireo fledgling, of 76 black-capped vireo nests 15 were successful, a nest success of 19.7%, a figure comparable to that of the last-named study.

Table 5 gives data concerning the causes of reproductive losses. Of six nests abandoned before completion, four nests represented first nesting attempts, one was a late attempt, and one a second nesting. One other early nest was completed, but I found no evidence that eggs were deposited in it. It is possible that the eggs were removed by cowbirds before I visited it.

Loss of eggs before hatching amounted to 55.1% of all eggs laid. Of this loss (134 eggs in all), I at-

TABLE 5. Analysis of Nesting Success for Three Years.

Year.....	1954	1955	1956	1956	Totals
Locality.....	Okla.	Okla.	Texas	Okla.	
Nests started.....	29	25	29	—	83
Nests laid in.....	26	25	25	—	76
Eggs laid.....	85	83	75	—	243
Eggs lost.....	24	20	35	—	79
Eggs deserted.....	24	21	10	—	55
Eggs fully incubated.....	37	42	30	—	109
Eggs infertile or addled.....	6	6	2	—	14
Eggs hatched.....	31	36	28	—	95
Chicks lost at hatching.....	8	—	1	—	9
Chicks lost to predators.....	2	11	3	—	16
Chicks lost because of presence of cowbird chick.....	8	1	16	—	25
Chicks that died in nest.....	2	—	—	—	2
Chicks fledged.....	11	24	8	—	43
Nests successful in fledging young.....	5	7	3	—	15
Pairs successful in rearing at least one chick.....	6	17	6	17	46
Number of pairs observed.....	16	21	10	21	77

tribute 72.3% (97 eggs) to cowbird activity. This includes beak-gouged eggs found under and in nests, eggs which disappeared one at a time with subsequent laying of cowbird eggs, and eggs deserted because of cowbird activity. Pitelka & Koestner (1942) estimate that 17 of 26 (65%) Bell's vireo nests were unsuccessful because of cowbirds (four nests failed for other reasons). Ely (1957) found that 10 of 13 (77%) Bell's vireo nests were parasitized, and that only one parasitized nest was successful (the cowbird egg in this nest did not hatch). David F. Parmelee ascertained that 12 of 22 (54%) Bell's vireo nests at Norman, Oklahoma, in 1954, were parasitized. My own observations of Bell's vireo in Caddo County, Oklahoma, also indicate great losses of eggs and young because of cowbirds.

Eighteen black-capped vireo eggs (13.4% of those lost) were deserted because of my activities. I learned to be more discreet after the first season, and the loss was reduced from 10 eggs (three clutches) the first season to one egg (an incompleting clutch) in 1956. I do not believe that my activities caused any more losses to predators than there would have been had I not been present. I probably frightened away as many predators approaching nests as I led to nests. And in no nest near a blind erected for daily observation was there any loss as long as the blind was present.

Two eggs (1.4% of those lost) were lost to a fox squirrel (*Sciurus niger*), the only case of mammalian predation which I observed. Ten eggs (7.4% of those lost) were lost to other predators, very likely snakes. Entire clutches disappeared without a trace of disturbance about the nest, and this would suggest predation by snakes. Snakes were numerous in the area, and I caught a pilot blacksnake (*Elaphe obsoleta*) in the act of swallowing a nestful of young vireos. Seven eggs (5.2%) were deserted. One clutch of four was deserted when a leaf fell into the

TABLE 6. Food of Black-Capped Vireo.

Stomach no.	Total items	KIND OF FOOD (Estimated percentage of bulk of total contents)										
		Vegetable matter (seeds)	Animal matter (Invertebrates)									
			Spiders	Centipedes	Insects							
					Orthoptera	Neuroptera	Odonata	Hemiptera	Homoptera	Coleoptera	Lepidoptera	Diptera
1.....	9	5	—	—	25	—	—	—	—	20	50	—
2.....	22	50	—	—	—	—	9	—	—	1	40	—
3.....	23	60	5	—	—	—	—	5	—	—	30	—
4.....	8	—	—	—	1	—	—	—	5	9	85	—
5.....	6	—	5	—	—	—	—	5	—	5	85	—
6.....	6	—	20	—	—	—	—	—	—	80	—	—
7.....	2	—	—	50	—	—	—	—	—	—	50	—
8.....	13	1	—	—	—	1	—	—	—	40	50	8
9.....	10	5	—	—	—	—	—	15	—	15	60	5
10.....	11	—	—	—	—	—	—	5	15	20	60	—
11.....	10	—	5	—	—	—	—	—	5	50	40	—

Stomach number	Locality	Date
1	Caddo Co., Oklahoma	September 9, 1954
2	Nayarit, Mexico	December 28, 1955
3	Nayarit, Mexico	December 29, 1955
4	Coahuila, Mexico	June 17, 1956
5	Hays Co., Texas	July 9, 1956
6	Kinney Co., Texas	July 13, 1956
7	Uvalde Co., Texas	July 12, 1956
8	Caddo Co., Oklahoma	September 9, 1954
9	Sinaloa, Mexico	December 21, 1955
10	Coahuila, Mexico	June 18, 1956
11	Coahuila, Mexico	June 18, 1956

nest. Three eggs were deserted that were the fourth clutch of a pair of vireos that had already deserted three clutches as a result of cowbird parasitism.

During the nestling period, as during laying, the chief loss was due to cowbird parasitism. In all cases in which a cowbird chick occupied the nest, no vireo chicks survived. Predation of nestlings was, in nearly every case, I believe, by snakes. In 1956, in Oklahoma, three seven-day-old chicks in one nest were eaten alive by ants (*Crematogaster* sp.).

Toward the end of each breeding season, I surveyed the study areas and adjacent areas, and observed whether or not the adults were in attendance on juveniles. Since most early nestings were unsuccessful, few juvenile birds were independent of the adults by late July and early August. This survey served as another check on how successful the birds had been in rearing young. Of a total of 77 pairs surveyed, 45 (59.7%) were successful in fledging at least one young bird by the end of the breeding season (see foot of Table 5).

FOOD AND FEEDING

The black-capped vireo, an arboreal species, rarely leaves the trees and shrubs of its domain. It feeds mainly in the upper strata of this vegetation, glean-

ing insects that live on trees, especially oaks. I have never seen it feed on the ground. The bulk of its food is larvae, and most of these are Lepidoptera. I have seen it eating small butterflies (*Pieridae*) and once, a large dragon-fly (*Odonata*, *Aeschnidae*). The young, when small, are fed mainly small larvae, sometimes spiders, and small flies. As they grow, the items fed to them are larger; bigger larvae and such items as small grasshoppers and katydids are brought. As much as a third of their food may consist of orthopterans.

Table 6 presents an analysis of stomach contents from eleven black-capped vireos. Further identification of food items is presented in the thesis. All these specimens were collected between the hours of eight and ten in the morning. Two were taken in the northern part of the breeding range (Oklahoma), three in the central (Texas), three in the southern (Coahuila, Mexico), and three on the wintering grounds (Sinaloa and Nayarit, Mexico). The sample is much too small to give a complete picture of the food habits, but it does suggest that this vireo is not unlike other vireos in its feeding habits. Bunker (1910) suggested that *Vireo atricapilla* had a very restricted diet. This does not appear to be the case.

Most of the items found have been found in the stomachs of other vireos by Chapin (1925). Exceptions are the centipede, the tettigoniid, and the fulgorid. My captive thrrove on a variety of insects.

Despite the considerable variety in the contents of these stomachs, there is a great deal of similarity in the food of specimens collected in the same localities. What the species eats is no doubt influenced by the locality, the season, and the time of day. The stomach contents of an immature male and an immature female taken at the same locality on two subsequent mornings were very similar.

It appears, as is true of other vireos, that the black-capped vireo eats some vegetable matter in the fall and winter. Over 50% of the bulk of the stomach contents of two immature birds taken in Mexico in December was seeds. The weather was cool and these birds may have resorted to vegetable food in the absence of numbers of insects. An adult taken in a warmer locality a few days earlier had only two small seeds in its stomach. No vegetable matter was found in the stomachs of the specimens taken in summer.

In no stomach did I find any sand or gravel. It is true that the bulk of the food is soft in nature, and the birds do crush it quite thoroughly before eating it. The stomach is fairly muscular and the hard (sclerotized) parts of insects may serve as grinding material. My captive bird regularly cast up pellets composed of undigested hard parts of insects. Herrick (1901) mentions that vireos are known to regurgitate such pellets.

The black-capped vireo can live without having surface water available. Much of its food (insect larvae) has a high water content. The bird takes advantage of dew and rain when it occurs.

FALL MIGRATION

The young birds disappear from the breeding grounds first. They are followed by the adult females, then by the adult males, some of which remain longer than others. Fall departure appears to be less precipitous than spring arrival. The species has been recorded in Nayarit, Mexico, as early as August 27. A specimen taken on that date was a female. My latest central Texas date for a female in 1955 was August 28 (one bird, Kerrville). This must have been about the date of departure for the females of that area that year, for I looked for one every day for a month thereafter, but saw none. The latest date for a female at San Angelo, Texas, in 1884 was September 6 (Cooke, 1888). The last time a female was seen in my Oklahoma study area in 1954 was on September 9 (one bird).

As for males, my latest central Texas date for 1955 was September 11 (three seen, Hays County). The last male reported at San Angelo, Texas, in 1884 was seen September 25 (Cooke 1888). The last time a male was seen in my Oklahoma study area in 1954 was on September 17 (one bird).

SURVIVAL

In 1954, I banded 24 breeding adults (12 pairs) in the Oklahoma study area. In 1955 I found nine of the banded males (75%) and five of the banded females (41.6%) in the same area. One female banded in 1954 I did not see in 1955 but did find in 1956. So 15 (62.5%) of 24 birds are known to have survived for one year.

In 1955 I banded five adult males and nine adult females. Of these, four males and three females returned in 1956, an 80% return for males, 33.3% for females, 50% for both sexes.

In 1956, nine males and five females, 14 (50%) of the 28 birds known to be in the area at the end of the 1955 season, returned.

Birds returning for a third season (1956) included five males and two females, seven (29.1%) of the 24 birds banded in 1954. Thus from data obtained during three years of observation, 41.6% of the males and 16.6% of the females were three years old or older; 33.3% (males) and 25% (females) were two years old or older; and 25% (males) and 58.3% (females) were one year old, or older birds that had just entered the area. Theoretically, if the percentage survival of a species breeding at one year of age is 75, 25% of the population will be made up of birds one year of age, 19% of birds two years old, and 56% of birds three years old or older, with one bird in a hundred living to be 13 years old.

Using Birkitt's formula in modified form (Hann 1948) for calculating average age, that of a male *Vireo atricapilla* in the study area is estimated to be four to five years (survival rate, 75 to 80%), of a female, one-and-a-half to two years (survival rate, 33.3 to 41.6%).

I have not had any returns on banded fledglings, but this is not surprising for I banded only 30. Birds in their first breeding season probably have little chance to breed in the area in which they were reared because the older birds remain in, and defend, their own territories. Of 13 males and 10 females caught in 1956, only one pair were first year birds (8.6%).

The sex ratio for the Oklahoma study area in 1954 appeared to be 106 males to 100 females; in 1955, 100:100; and in the Texas study area in 1956, 131:100. Stewart & Aldrich (1951) found differences in sex ratio in vireos of other species were high. Nice (1937) observed that female "survival" was two-thirds to three-fourths that of males in the song sparrow (*Melospiza melodia*) and that the sex ratio was a little greater on the male side. The difference in returns for females (in this study 55.5% in 1955 and 41.6% in 1956 of those for males) might be explained by their elusiveness and lack of attachment to their territories.

The black-capped vireo appears to be unusually free of ectoparasites. I have never found a bird or a nest that had mites, mallophaga, or parasitic diptera. This statement is the more valid in view of the fact that within the study area other birds and their nests had parasites of various sorts.

One adult male black-capped vireo disappeared from his breeding territory. This was the only adult bird under observation that may have died during the breeding season in the course of this study. Two nestlings died of unknown cause(s) in 1954.

Some birds had foot trouble as a result of my placing the color bands below the metal bands (done to make the birds individually recognizable in the field). One male had a wisp of plant fiber or spider web tightly bound about his ankle which was swollen as a result.

SUMMARY

Vireo atricapilla breeds locally from north central Oklahoma, through central Texas, to north central Mexico (Coahuila). It winters on the west coast of Mexico from southern Sonora to Guerrero. In the breeding area it is usually found at elevations of 1,000-2,000 feet, but may occur at 5,500-6,000 feet in the southern part of its range. In winter it occurs at elevations from sea level to about 3,000 feet.

The breeding range at present is smaller than it was around 1900. Long term trends toward higher temperatures and less precipitation may account for a reduction in the habitat at the western and northern edges of the breeding range. A list of other birds found on territories of black-capped vireos is given. The ecological relationships of *V. bellii*, *V. griseus*, *V. huttoni*, and *V. vicinior* are briefly discussed.

Vegetation of the habitat was studied in two areas in which the species is successful, and in areas at the edge of the bird's range. The size and arrangement of vegetation appears to be important. The species prefers scrub-oak growth of irregular height and distribution. Throughout the bird's breeding range several different plant (species) associations are found, but these associations intergrade with each other, and their members may be considered as ecological counterparts. The type of vegetation occupied occurs very locally throughout the area in which the climatic conditions are suitable. The habitat must cover a rectangular, rather than a linear area. Eroded slopes often provide edaphic conditions which favor such habitat. Presence of surface water is not necessary.

Monthly means of temperature in the areas occupied by the bird (both in summer and winter) were between 63° and 87° F. Extreme lows of temperature were well above freezing (37° F.). Monthly means of precipitation were between zero and five inches. Precipitation is important indirectly because of its effect on vegetation. No loss of any kind from rain, wind, hail or severe dust storms was observed.

The black-capped vireo appears to be restricted in its distribution by rigid requirements of vegetative and climatic factors. It does not adapt to modified conditions and therefore becomes very limited in its distribution.

An intensive study was made of the life history. It was found that *Vireo atricapilla* migrates northward in spring, arriving in the southern part of the breeding grounds in March; in the northern part, in

late April. The male establishes a territory of two and one-half to four and one-half acres by song and pouncing. All activities are carried out on this territory. Individual birds return to the same territories year after year. Mates may be changed between broods or between seasons, but usually a pair remains together for a season. The female is courted by song and display.

Nests are placed in crotches of limbs usually one to four feet above the ground. Oaks are usually chosen. There is a tendency for vireos to re-use nest sites season after season. The nest is typically vireonine. It is built of materials available nearby, and both male and female participate in nest-building. Construction may take as little as four days or as long as 16 days.

Laying occurs at about 6:00 a.m. CST (during June, in Oklahoma) on consecutive days. The peak of laying is in May in Texas and in June in Oklahoma. A clutch consists of three or four eggs. The eggs are white, immaculate, and average approximately 17.6×13.1 mm. They weigh about 1.5 grams at laying. Incubation begins after the laying of the second or third egg. In general the parent birds incubate alternately throughout the day. The female incubates at night. The incubation period varies from 14 to 17 days.

At hatching, the chick is completely naked and blind, and weighs about one gram. It gains about a gram a day until it weighs seven or eight grams. Its feathers unsheath on the eighth day. It leaves the nest at 10 to 12 days. The postjuvinal molt begins at the age of two weeks. Forty-four days after leaving the nest, one young bird was independent of its parent. The young in the nest are cared for by both male and female adults. The female does all the brooding. The male brings about three-fourths of the food to the young. Fledglings are cared for by both parents for four to seven days, then the female begins another nesting. She either does all the incubation and cares for the young of the second brood or mates with another male while her first mate is occupied with the care of the fledglings. The young are fed 0.8 to 2.6 times an hour. As the young grow, the number of trips the adults make to bring food to them remains the same, but larger items are brought. One cowbird chick requires as much food as four vireo chicks.

Of 243 eggs, 43 (17.6%) were successful to the stage of nest-leaving. Of 75 nests, 15 (20%) were successful in producing one fledgling. A survey of pairs was made late in the breeding season. Of 77 pairs, 45 were successful in fledging at least one young bird. The greatest losses in eggs and young were caused by cowbird activity. Ninety-seven eggs (72.3% of those lost), and 25 (29.7% of the viable chicks) chicks were lost because of cowbirds. The Bell's vireo appears to sustain such losses also.

Vireo atricapilla does not appear to be restricted by diet. Food found in the stomachs of 11 specimens was similar in type and amount to that found in

stomachs of the Red-eyed Vireo (Chapin 1925). The bulk of the food consists of larvae of Lepidoptera and of small Coleoptera. Interchange of young black-capped and Bell's vireos showed that each of these could subsist as nestlings and fledglings on the food of the other. A captive fledgling *atricapilla* thrived on a variety of insects.

Fall migration begins in August. The earliest known arrival on the wintering grounds is August 27th. No black-capped vireos have been seen on the breeding grounds after September.

Between 50 and 60% of the breeding birds were new to the Oklahoma study area each season. Between 75 and 80% of the banded males returned for a second season, but only 33.3 to 41.6% of the females returned. The difference may be accounted for by the elusiveness of the female and by failure of the female to return to the same area. Twenty-nine % of the banded birds returned for a third season (41.6% of the males, 16.6% of the females). One pair (8.6%) of 23 birds trapped in 1955 were birds breeding for the first time. The sex ratio varied from 100 (males):100 to 131:100. A few males did not find mates during some seasons.

The species appears to be unusually free of ectoparasites and disease. Few, if any, predators take adult vireos. Loss during breeding season may have amounted to one adult from 150 birds in three seasons' observations.

No factor was found in the life cycle that could account for its limited numbers. Its habits are similar to those of other vireos. Its nesting success is low compared to that of other passerines, but not lower than that of a closely related, more widely distributed species, *Vireo bellii*. The black-capped vireo suffers large reproductive losses because of cowbird parasitism, but so does Bell's vireo. The black-capped vireo's low reproductive success is probably compensated for by the survival rate and longevity of adults. The species appears to be as long-lived as certain more widely distributed forms (Hann 1948, Nice 1937).

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THE VEGETATION OF GOUGH ISLAND

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INTRODUCTION

Gough Island is an isolated mass of volcanic rock in the South Atlantic Ocean in position 40° 19'S., 9°57'W. The Tristan da Cunha islands (37°S., 12°W.) which lie 370 kms to the North-north-west are the only land within 2000 kms. The nearest points on the surrounding continents are approximately 2400 kms (South Africa), 3000 kms (South America), and 3200 kms (Antarctica) distant from Gough Island (Fig. 1).

The island was discovered by the Portuguese in the first decade of the 16th century, probably in 1505 (Uhlen 1939), and named Goncealo Alvarez

after its discoverer. It was sighted from the barque *Richmond* (Capt. Gough) in 1731, and renamed. The island was uninhabited when first discovered, and few visits are recorded until the 19th century, when parties of sealers are known to have lived ashore during the years 1810-11, 1888-89 and 1891-92. A diamond-prospecting party lived on the island for 5 months in 1919. All these visitors lived in caves or huts, either at Goncealo Alvarez on the East coast or at Cave Cove or Lot's Wife Cove on the North (Fig. 3). They grew potatoes near their dwellings, but they imported no grazing animals and their activities had very little effect on the native vegetation.

Apart from a few notes in the diary of a member of the sealing party of 1888-89 (Verrill 1895), nothing was recorded concerning the plant life of the island until the visit of the *Scotia* in 1904 (Rudmose Brown 1905a). Subsequent visits made during the autumn or early winter by vessels returning from the Antarctic, were paid by the *Quest* in 1922 (Wild 1923a, 1923b), the *William Scoresby* in 1927 (Gunther 1928), and the *Thorshavn* in 1933 (Christensen 1935). Collections of plants made on these occasions have been described by Rudmose Brown (1905b), Wilkins (1925) and Christophersen (1934). A few brief notes were also made in some of these papers on the lowland vegetation types, but no systematic description of the vegetation of the whole island has previously been published.

Gough Island was annexed by Britain in 1938, and with Tristan da Cunha, is a dependency of the Crown Colony of St. Helena. In 1955-56 it was mapped and studied in detail by a small British Expedition, the Gough Island Scientific Survey, of which the author was a member. This Expedition established a meteorological station which was sub-



FIG. 1. The Southern Hemisphere, showing the positions of Gough Island and the other islands mentioned in the text.

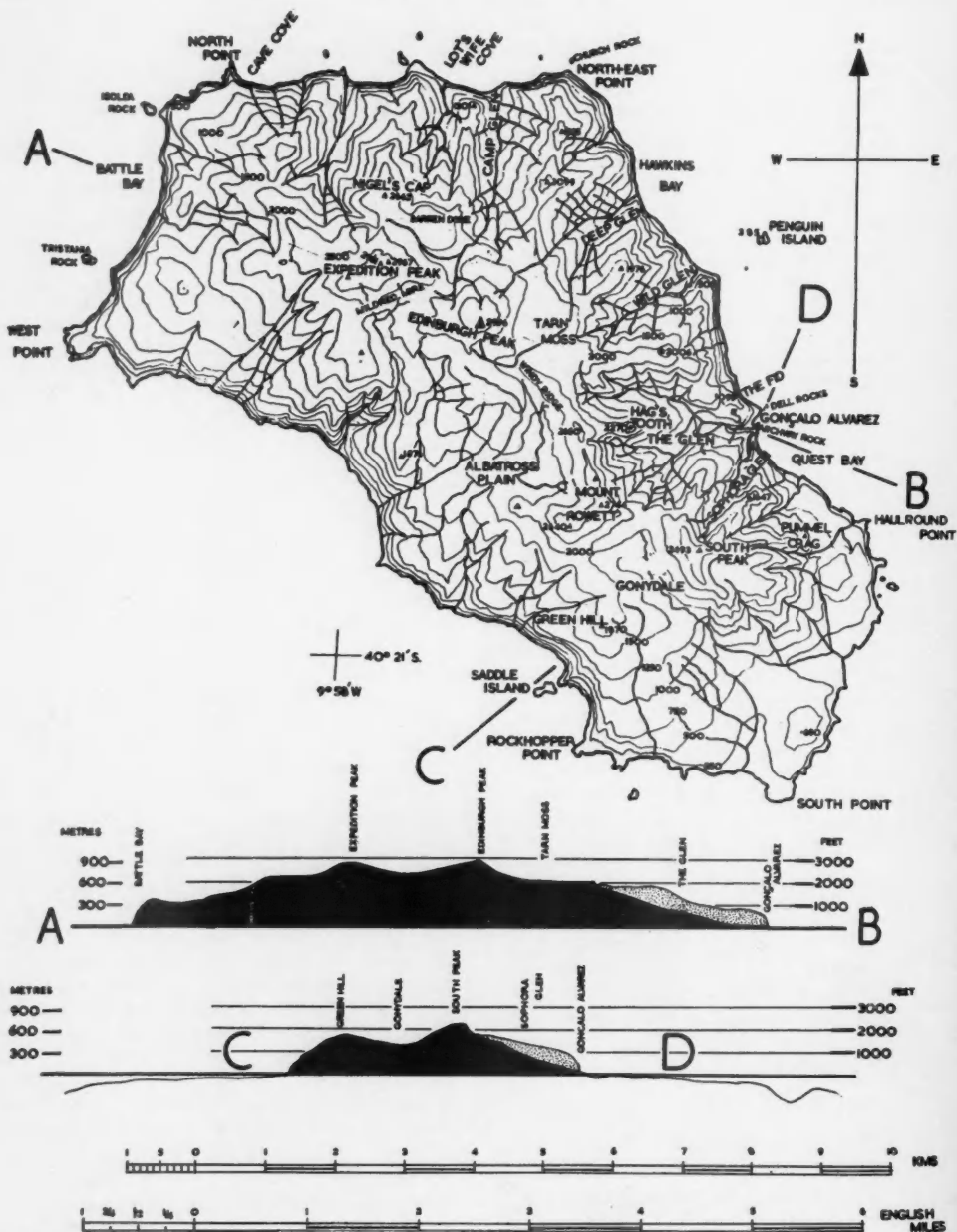


FIG. 3. Map and profiles of Gough Island. Map from the Gough Island Scientific Survey 1955-56 (Heaney & Holdgate 1957); heights in feet, contour interval 250ft. Profiles on the same scale as the map, with vertical and horizontal scales equal. Submarine profiles approximate, by interpolation from South African chart no. 23.



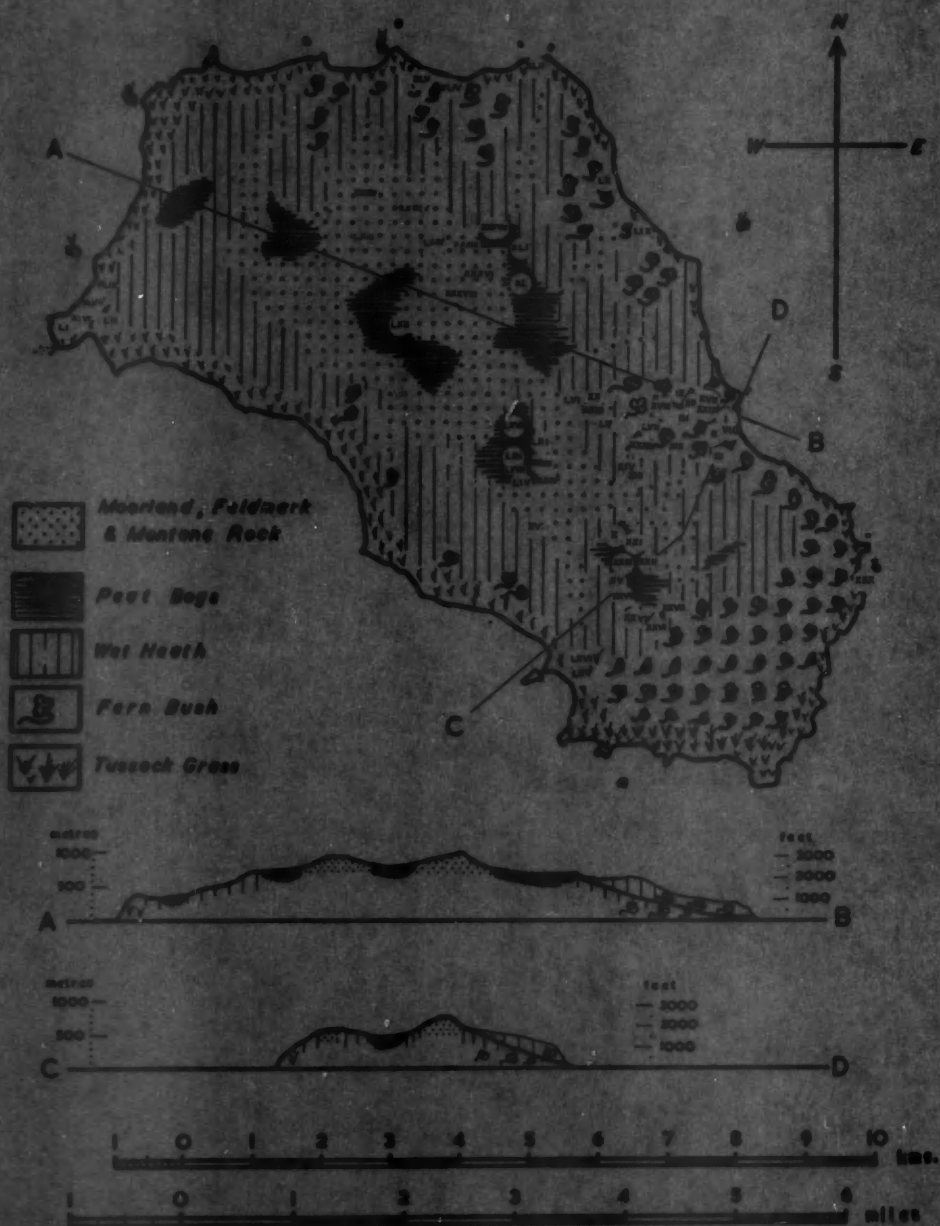


FIG. 2. Vegetation map and profiles of Gough Island. Roman numerals on the map mark the positions of quadrats mentioned in the text.

sequently maintained by the South African Weather Bureau. The introduction of sheep and poultry to supply the station with food, and the regular visits of ships relieving the station personnel and crew-fishing around the island have led to the introduction of alien plants, and changes in the natural vegetation are therefore to be expected in future (pp. 360-361). The present paper is thus not only the first systematic account of the island's vegetation, but a background against which future man-induced changes may be viewed.

The history of Gough Island, together with general accounts of its topography and biology and the findings of the 1955-56 Survey, have been given by Heaney & Holdgate (1957) and Holdgate (1958).

GENERAL DESCRIPTION OF THE ISLAND

TOPOGRAPHY

Gough Island is approximately rectangular in plan, 13 km long and 5 to 6 km broad (Fig. 3). From a plateau at 600m above present sea level, the highest point, Edinburgh Peak, rises to 910m. Eight deep canyons cut back into the centre of the island from the North and East coasts: these "glens" are up to 2 km in length, and about 450m deep, and they are divided from one another by steep-sided ridges running out from the plateau and the central mountains.

To the West of the island, rolling slopes from the plateau end in cliffs of 300 to 450 m height, and a mean angle of slope of c. 50° from the horizontal. These Western cliffs are little cut into by valleys from seaward. The South of the island slopes more gently from the plateau to the sea, although the ground is very broken and cut up by small gullies, and it includes the only extensive area of land below the 300m contour.

The coast is everywhere cliffed and steep, with a number of offlying sea-stacks. Narrow boulder beaches are found at the foot of most of the cliffs; plunging cliffs are more-or-less confined to the headlands. There are no coral reefs, and soundings suggest that the submarine slopes fall away steeply outside the platform of marine erosion round the shoreline (Fig. 3).

GEOLOGY

The rocks of Gough are all volcanic, and probably of late Tertiary age. LeMaitre (1960) has recognized five stages in the formation of the island, involving the build-up of a basaltic mass, its partial destruction in an explosion which deposited deep layers of tuff and the extrusion of much trachyte, the formation of further basaltic lava flows, and the still later formation of dome-shaped masses of trachyte, and the final capping of Edinburgh Peak with basalts and cinders. There are no signs of any volcanic activity at present, and none has been recorded since the island was first discovered, but bands of volcanic ash which probably originated

from the island itself, occur in peat which has been dated at 2345 (± 120) years before present (Godwin & Willis 1959).¹ The age of Gough Island in relation to that of its present vegetation is discussed below (p. 41), and by Hafsten (1960a & 1960b).

CLIMATE

Gough Island has a temperate climate, with a mean annual air temperature (at Goncalo Alvarez, sea level) for the years 1956 and 1957 of 11.7°C (53.1°F). The mean annual rainfall for the same place and period was 3225 mm (129 in.), and the relative humidity 81% (Figs. 4, 5). The climate is extremely oceanic: Kotilainen's index of oceanicity (Godske 1944) is c. 590 at Goncalo Alvarez (compared to less than 500 for the wettest parts of the Scottish Highlands, and less than 420 for Western Norway (Poore & McVean 1957). Snow lies on the mountains during a few of the winter months above about 450m, but the air temperature probably never falls to freezing point at sea level.

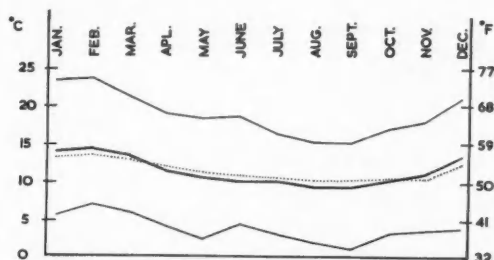


FIG. 4. Monthly mean air temperatures and monthly extremes at Goncalo Alvarez weather station, for the 2 yrs 1956-57. The dotted line shows the mean monthly sea temperature at Goncalo Alvarez beach for the same period.

¹ The recent volcanic activity on Tristan da Cunha has led to a re-assessment of the evidence concerning vulcanicity in the islands of the Tristan group, and a re-examination of the peat profiles from there, and from Gough Island. This information has a direct bearing on the vegetational history of Gough Island. The present state of knowledge is as follows.

Before the present eruptions on Tristan, there were no authenticated accounts of any volcanic activity in the islands of the Tristan group, or on Gough Island, since their discovery in 1506; and certainly none has occurred in the Tristan group since 1810. Bands of volcanic ash in the peat were "frequently observed by the Norwegian expedition to Tristan da Cunha in 1937/38, but no systematic registration or mineralogical investigations were carried out" (Hafsten 1960b). Ash bands have been reported at about 80 cm from the peat surface in Nightingale Island (Hafsten 1960b), and may be present at a depth of 135 cm in the Albatross Plain peat on Gough Island; but pollen analyses of peats above and below these depths reveal that any volcanic activity had a negligible effect on the plant life of the islands. Further ash bands occur in the peat at Soggy Plain, Tristan, at 170-180 cm and at 250-255 cm below surface. The upper of these bands is at the same depth as the ash layer from Albatross Plain, Gough Island, which has been carbon-dated at 2345 yrs (± 120) before present. It is therefore likely that there was some minor and local volcanic activity on Tristan and Gough about 2400 yrs ago, but this was not severe enough to destroy the vegetation on either island. The deeper ash deposit at 250 cm on Tristan may coincide with the bottom of the peat profile on Gough which has been dated at 4720 yrs (± 130) before present. Both may possibly represent an earlier phase of volcanic activity at this time.

There is no definite evidence from the peat deposits on any of the islands, of any vegetation more than 5000 yrs old, but more work needs to be done on the dating of the lower layers of peat. The general picture that emerges, throughout the Tristan-Gough group, is of intermittent volcanic activity during the last few thousand years, which has had little effect on the islands' vegetation.

Much of the rainfall is orographic, and at 600m above sea level in the North of the island by the Barren Dome, the rainfall during eight periods from December 1955 to April 1956 was about $1\frac{1}{2}$ times that recorded during the same periods at Goncalo Alvarez on the East coast.

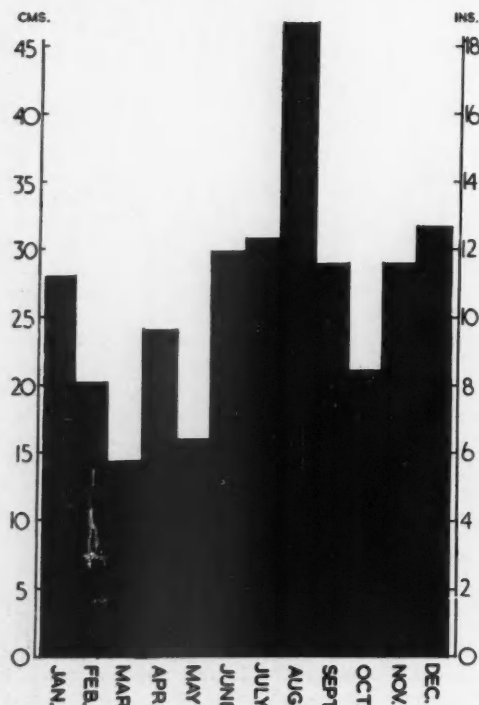


FIG. 5. Monthly mean rainfall at Goncalo Alvarez weather station for the 2 yrs 1956-57.

The weather is dominated by depressions passing over the island from West to East, and producing unsettled stormy weather with strong winds and heavy rain. The prevailing wind is westerly, and much salt spray is undoubtedly swept up the western cliffs and deposited on that side of the island. More easterly winds occur in the winter months, with the northward shift of the depression-tracks.

Although it is clear from the sea temperatures (Fig. 4) that the island lies between the sub-tropical and Antarctic convergences, and is therefore in the "sub-Antarctic" zone (Deacon 1960), it is misleading to refer to its climate—still less its vegetation—as "sub-Antarctic" in common with the colder islands of higher latitudes. The climate and vegetation of Gough Island are essentially temperate (Wace 1960).

SOILS

There are few developed mineral soils on Gough Island. Peat accumulation is everywhere rapid, except where retarded by exposure, and peat blankets most of the rock.

In the lower parts of the island, the constant slipping of accumulating peat from the steep sides of the Glens prevents the development of stable profiles on the slopes, and the surge of storm-water runoff also prevents the establishment of mature layered profiles in the valley bottoms. The plateaux and mountain valleys are covered in deep peat, which lies directly on the rock, with no intervening fossil soils. Only on the exposed mountain ridges, and on the upper slopes of the highest peaks, is a thin mineral soil found which generally consists of a shallow mixture of coarse rock fragments and humus without any signs of podsol formation. These upland soils are similar to those described by Taylor (1955) from Macquarie Island as "Dry Tundra Soils"; they are the only soils on the island which contain substantial numbers of earthworms (Holdgate 1960). A few agglomerate soils, with some iron-pan formation, were seen in small areas of raised beach near North-East Point, but apart from these coastal soils, podsoles were not found. Sandy beaches are infrequent and ephemeral, and there are no dunes or other wind-blown sands on the coasts or elsewhere.

A comparable absence of developed soils has been noted from Campbell Island (Marshall 1909) and Auckland Island (Speight 1909), in somewhat similar climatic conditions. Tristan da Cunha is also largely covered in peat, and lacks mature soils, although podsolised soil profiles have formed beneath the coastal plains, probably as a result of the destruction of vegetation following human settlement.

SCOPE OF THE PRESENT PAPER AND METHODS EMPLOYED

The data on which this account is based were collected on Gough Island by the author between November 1955 and May 1956. All the ground over 600m above sea level was explored, and the remainder was seen or traversed, but below 600m most of the detailed sampling was done in The Glen (Fig. 3). The low ground to the South of the island, and the smaller Glens of the North and East coasts were not examined in detail; the precipitous and broken terrain and the very dense vegetation in these parts, would make their detailed exploration a very long task in the prevailing weather conditions. The following descriptions are therefore more in the nature of a detailed reconnaissance of the vegetation, rather than an exhaustive and systematic description of all the plant communities of the island.

A mass-sampling method, using about 70 10-m quadrats, was employed. The positions of those quadrats from which plant lists are quoted in the text, are plotted in Roman numerals on the vegetation map of the island (Fig. 2). No attempt was made to achieve a random dispersal of the sample quadrats, nor to estimate objectively the number of differing vegetational units on the island.

Within the sampled quadrats, percentage cover for the component species was estimated by eye, for each separate layer of the community. These figures for percentage cover are quoted in the lists in the text. Symbols have been used in the lists to indicate coverages of less than 5%, thus:

- ++ scattered occurrences within a quadrat
- + a single occurrence within a quadrat.

An asterisk against the name of any species, indicates that that species is not native to Gough Island, but has been introduced by man.

A systematic list of the vascular flora of Gough Island, together with the authors of the species, is given at the end of this paper. Many of these species belong to genera with a Southern cold temperate or sub-Antarctic circumpolar distribution. Although the names that are given here are the best at present available, it is likely that fuller collections from other southern islands will lead to a revision of the taxonomy and nomenclature of at least some of them.

VEGETATION

Gough Island bears five physiognomically distinct types of vegetation, or *formations* (Warming 1925), whose distribution is shown in the map and profiles (Fig. 2). Every formation comprises several different communities, or *associations*, each of which is characterized by a different dominant species or group of species. These associations, which are used as the units of description in the following accounts, are grouped in their formations as follows:

Tussock Grassland

- Poa flabellata* tussock
- Spartina arundinacea* tussock

Fern Bush

- Histiopteris incisa* fernbrake
- Blechnum palmiforme* heath
- Phyllica arborea* bush

Wet Heath

- Blechnum palmiforme* heath
- Empetrum rubrum* heath
- Grass and Sedge heath

Moorland, verging to Feldmark & Montane Rock
Rhacomitrium-Empetrum moorland
Agrostis carmichaelii moorland
 Feldmark and montane rock communities

Peat Bogs

- Sphagnum montane valley bogs
- Bryales-Hepaticae plateau bogs
- Bog streamside communities

As on Tristan da Cunha (Wace & Holdgate 1958), the species-poverty of the flora, and the consequently high ecological amplitude of the native species, makes community differentiation and description difficult,

since very few species are characteristic of any single association. Environmental, physiognomic, and floristic differences are all used therefore to distinguish the communities in the following descriptions.

TUSSOCK GRASSLAND

Communities of large grasses forming stout tussocks up to 2m tall, cover most of the cliffs and offlying sea-stacks, and are characteristic of sea-elephant wallow grounds and penguin rookeries round the coasts.

Poa flabellata TUSSOCK

Poa flabellata forms dense and sometimes pure communities on the Western and Northern cliff-slopes (Fig. 6.), and also above the cliff-tops on some of the more level ground below 300m. The tussocks are up to 1.5m in height, including fibrous stools which may be as much as 0.6m high and 0.4m in diameter. Thick masses of leaves from adjoining tussocks interlace to form a closed community in which there are often no associated species. In one such community above West Point (LI), there were 30 tussocks in an area of 34 sqm, and the dry peat on which they were growing was entirely composed of the fibrous remains of the grass leaves, about 15cm deep. The peat and the lower parts of the stools contained a number of nesting burrows of the Greater Shearwater (*Puffinus gravis*).



FIG. 6. Community of pure *Poa flabellata* at 170m above sea level near West Point. Quadrat site LI. (Compare Taylor 1955; plate 4).

Mixed communities in which *Poa flabellata* is associated with *Apium australe*, *Spartina arundinacea*, and *Scirpus* spp. are typical of the broken ground on the drier parts of the Western and Northern cliffs. The overall slope of these tussock-covered cliffs varies from about 45° to 70° from the horizontal. There are few permanent streams, but runoff of surface water has formed small gullies, and channeled the peat between the tussock stools.

In the damper gullies which are constantly flushed by water draining from the Wet Heath above, more species are found. In one area at a height of 180m opposite Tristania Rock, on a slope of 60°, there is some soil creep and the vegetation is very insecurely rooted. A 10-m quadrat (XLIX) here gave the following lists of species, with the indicated coverages:

<i>Poa flabellata</i>	50%
<i>Apium australe</i>	20%
<i>Chenopodium tomentosum</i>	10%
* <i>Rumex obtusifolius</i>	++
<i>Carex insularis</i>	+
<i>Dryopteris aquilina</i>	+
<i>Histiopteris incisa</i>	+
* <i>Sonchus oleraceus</i>	+
<i>Scirpus</i> sp.	+
<i>Hydrocotyle leucocephala</i>	+
<i>Acaena sarmentosa</i>	+
<i>Rumohra adiantiformis</i>	+
<i>Gnaphalium pyramidale</i>	+
<i>Cotula goughensis</i>	+
<i>Agrostis media</i>	+
<i>Elaphoglossum laurifolium</i>	+
<i>Hypolepis rugosula</i>	+

Poa flabellata is also the principal dominant in some sheltered hollows at about 490m above sea level, to the South and West of Gonydale. These hollows are up to 20m deep, and filled with large rocks and boulders, which are overgrown by *Poa flabellata* tussocks, associated with *Empetrum rubrum*, *Blechnum penna-marina*, *Apium australe*, *Scirpus* sp., *Asplenium obtusatum* and *Dryopteris aquilina* (XXVI). *Poa flabellata* is confined to the areas of good drainage, and the bottoms of the hollows and the surrounding areas support wet bryophyte communities which are more typical of the surrounding Wet Heath. The crevices between the boulders are the resort of numerous *Procellariidae*, and there is much guano around the entrances to their burrows.

Spartina arundinacea TUSOCK

The large ligneous grass *Spartina arundinacea* occurs sporadically in all the major plant communities below 600m. In Sphagnum flushes in the Fern Bush, and in the Wet Heath communities, it forms no stool above the surrounding peat, but round the coasts in penguin rookeries and between the wallowholes of Elephant Seals it dominates open communities with tussocks up to 3m in height with thick woody stools and a crown of long stiff stems and leaves. Penguin Island is largely covered by dense *Spartina* tussock, in which the stools are up to 1m in height, and so set apart from one another that the interlacing foliage from adjoining plants excludes the light from a maze of dark tunnels between the stools.

Unlike *Poa flabellata*, *Spartina arundinacea* does not form extensive pure communities on the maritime cliffs, but dominates mixed communities on some of the Western cliff-slopes, as in a 10-m quadrat (LII) at 150m above West Point:

<i>Spartina arundinacea</i>	35%
<i>Carex insularis</i>	30%
<i>Poa flabellata</i>	15%
<i>Acaena sarmentosa</i>	10%
<i>Apium australe</i>	5%
<i>Dryopteris aquilina</i>	++
<i>Hypolepis rugosula</i>	+

Several centimetres of litter overlies a damp compacted peat which is up to 30cm deep between the rock outcrops. In a few places where sufficient light penetrates to the tussock stools, *Callitriche christensenii*, *Hydrocotyle leucocephala* and *Marchantia polymorpha* are found.

PENGUIN ROOKERIES

It is estimated that about two million rockhopper penguins (*Eudyptes cristatus*) breed on Gough Island (Swales, in preparation). During the summer months they occupy large rookeries around the accessible parts of the coast, and as high as 100m up the cliffs. There are large rookeries at Rockhopper Point and in the Sophora Glen, and smaller ones near West Point, South Point, in Hawkins' Bay and elsewhere.

In the densely populated parts of these rookeries there are often no vascular plants, and the rocks are covered with a layer of guano, feathers, and redeposited peat. Elsewhere, *Spartina arundinacea* and *Poa flabellata* form luxuriant tussocks on the heavily dunged ground. Small tufts of *Scirpus thourarsianus* and *S. sulcatus* overlying the rocks, and *Asplenium obtusatum* and *A. alvaradense* on the sides of the tussock stools are often the only associated species.

Two 10-m quadrats in penguin rookeries yielded the following lists of species:

	XLVII (West Point)	XXIX (The Glen)
<i>Poa flabellata</i>	45%	25%
<i>Scirpus</i> spp.	—	10%
<i>Spartina arundinacea</i>	5%	5%
<i>Callitriche christensenii</i>	—	5%
<i>Asplenium obtusatum</i>	—	++
<i>Apium australe</i>	—	+
<i>Histiopteris incisa</i>	—	+
<i>Hypolepis rugosula</i>	—	+
Bare ground	50%	40%

Both the rookeries are terraced, the level ground where the penguins stand being covered with compacted guano and bare of vegetation, and the rocky banks and gullies supporting the plants. Abandoned rookeries, and the less densely-populated parts of inhabited rookeries, are colonised by *Cotula goughensis*, **Rumex obtusifolius* and **Poa annua*.

ELEPHANT SEAL WALLOW-GROUNDS

Narrow rocky beaches backed by cliffs surround most of the island, but there are a few areas of flat ground near sea level where Elephant Seals (*Mirounga leonina*) haul out to breed and moult. These areas are characterised by open *Spartina arundinacea* communities in which much of the

ground vegetation between the tussocks is destroyed by the movements of the animals, and in which depressions in the ground are occupied by muddy wallows where the seals moult in summer.

Above the high-tide mark in Hawkins' Bay, but within reach of the storms (inferred from the presence of driftwood), there are numerous wallows amongst the widely-spaced *Spartina* stools. A 10-m quadrat (LIX) included the following species:

<i>Spartina arundinacea</i>	15%
* <i>Agrostis stolonifera</i>	40%
<i>Cotula goughensis</i>	30%
* <i>Rumex obtusifolius</i>	5%
<i>R. frutescens</i>	++
* <i>Poa annua</i>	5%
<i>P. flabellata</i>	+
<i>Callitriche christensenii</i>	++
<i>Scirpus</i> sp.	+

Many of the smaller colonists are human introductions and frequenters of waste ground around sealers' huts, old potato patches, etc. In some of the adjoining areas, most of the ground flora has been destroyed by the movement of the seals, and the ground is strewn with the remains of *Spartina* stems and leaves (Fig. 7).



FIG. 7. Tussocks of *Spartina arundinacea* in Elephant-Seal wallowing ground above the beach at Hawkins' Bay. The ground is strewn with *Spartina* stems, and some driftwood. *Cotula goughensis* and *Rumex obtusifolius* beneath the tussocks to the left. *Phylica arborea* thickets on slopes in the background.

SERIAL STAGES LEADING TO TUSOCK GRASSLAND

The major Tussock Grass communities on the island are developed upon slopes of about 50° from the horizontal on the Western Cliffs. Falls of rock and the peeling away of the accumulated plant remains from the rock surface ("peatlips") initiate recolonisation stages in which *Scirpus* spp. and *Campylopus lusciniatis* are important primary colonists in the rock crevices. *Chenopodium tomentosum* is also a frequent colonist of plant and rock debris at the bottom of these peatlip sites.

In a 10-m quadrat on a small peatlip site at

110m on the cliffs above West Point, smooth trachyte slabs from which the overlying grass-peat had slipped away, were being recolonised by: *Scirpus* spp., *Poa flabellata*, *Chenopodium tomentosum*, *Apium australe*, *Dyopteris aquilina*, and **Poa annua*, which were spreading on to the area by seed or spore. Later stages in the succession seen nearby involved the vegetative spread of *Poa flabellata* and *Chenopodium tomentosum* from adjoining climax communities, and the disappearance of *Scirpus* spp. and the ferns in competition with the tussock grass and *Apium australe*.

HABITAT FACTORS OF TUSOCK GRASSLAND COMMUNITIES

The preceding account has shown that *Poa flabellata* tussock communities are characteristic of steep well-drained coastal slopes where the water runoff is rapid and the peat dry and stable. But although predominantly a plant of exposed maritime cliffs, the *Poa* does dominate some sheltered inland communities where these are well-drained, and wet peat cannot accumulate. The large tussock-habit is well adapted to survive the combination of rapid water runoff (between the tussock stools), secure anchorage on steep slopes (by its efficient rooting into the rock crevices), and extreme exposure (because it does not develop a great weight of foliage above the ground or wet peat on the rock surface). The ecological distribution of *Poa flabellata* on Gough Island resembles that of the same species in the Falklands (Skottsborg 1913) and South Georgia (Skottsborg 1912), and is in accordance with its known ecological preferences when grown in the Scottish Hebrides from seed of Falkland plants (Dallimore 1919). It seems that *Poa flabellata* tussock is a type of sub-maritime grassland, the ecological equivalents of which are one of the characteristic features of the coastal vegetation of the Southern temperate and sub-Antarctic islands (Wace 1960).

Spartina arundinacea tussock is extensively developed and most luxuriant in coastal areas where there is heavy animal trampling and manuring. Its very tough woody tussock is well-adapted to survive the trampling and crushing which destroys its few potential associates in the more densely populated Elephant-seal wallow grounds, and *Spartina* tussock grassland is predominantly a biotic climax community.

FERN BUSH

Thickets of *Phylica arborea* interspersed with *Histiopteris incisae* fernbrake and *Blechnum palmiforme* heath form a very dense vegetation below 300m in the North and East coast glens, and to the South of the island, and also in some small Western cliff gullies. The *Phylica*, *Blechnum*, and *Histiopteris*-dominated communities form a mosaic, here collectively termed Fern Bush.

Histiopteris incisa FERNBRAKE

Histiopteris incisa occurs sporadically in most of the more sheltered communities up to 600m above sea level. In the Glens and on the Southern slopes it dominates extensive areas, often with few associates. In a 7-m quadrat at 15m above the sea near Goncalo Alvarez (I), loosely packed and moist peat up to 1m deep is covered by a dense layer of *Histiopteris* with fronds as much as 90cm long. There are few field layer associates, but *Brachythecium* cf. *rutabulum* and seedlings of *Apium australe* cover the peat surface in the spring, and *Apium* is probably a more important constituent of the field layer in the autumn and winter when the fern fronds have died down. The following species were recorded from the quadrat in December:

	field layer	ground layer
<i>Histiopteris incisa</i>	90%	—
<i>Apium australe</i>	5%	10%
<i>Carex insularis</i>	+	—
<i>Hypolepis rugosula</i>	+	—
* <i>Rumex obtusifolius</i>	+	—
<i>Scirpus sulcatus</i>	+	—
<i>Brachythecium</i> cf. <i>rutabulum</i>	—	90%

Elaphoglossum laurifolium and *Asplenium alvaradense* are abundant on dead *Phylica* logs, and *Lophocolea undulata* is epiphytic on the *Histiopteris* stipes.

Communities of this type in which *Histiopteris* is overwhelmingly the dominant species are common in the lower reaches of the Fern Bush in the Glens, where the slope of the ground does not exceed c. 45°. Where the surface is very uneven, and where more light reaches the ground, *Asplenium alvaradense* dominates the ground layer in association with *Brachythecium* sp. A 10-m quadrat at 110m in The Glen (XVIII) gave this typical list of species:

	field layer	ground layer
<i>Histiopteris incisa</i>	90%	—
<i>Blechnum palmiforme</i>	5%	—
<i>Asplenium alvaradense</i>	—	90%
<i>Brachythecium</i> cf. <i>rutabulum</i>	—	10%

together with *Elaphoglossum laurifolium*, *Asplenium obtusatum* and *Hypolepis rugosula* on the peat hummocks which overlay the buried remains of *Phylica* and *Blechnum palmiforme* trunks. At the time of the investigation (Feb.), this quadrat contained several occupied burrows of the soft-plumage petrel (*Pterodroma mollis*) with eggs. This species, and the broad-billed prion (*Pachyptila vittata*) are abundant in the Fern Bush peats, and their burrowing activities are an important factor contributing to the instability of the peat on steep slopes.

On the very broken slopes below 300m in the South-East of the island, *Histiopteris* is partially replaced in the Fern Bush by *Asplenium obtusatum* and *Rumohra adiantiformis*. Both of these species can withstand considerable exposure to salt spray, and the peat on which they grow is much drier than in the more sheltered and constantly humid Glens.

Large patches of *Empetrum rubrum* and *Carex insularis*, sometimes overlain by straggling masses of *Acaena sarmentosa*, grow between the *Phylica* thickets. Typical *Histiopteris* fernbrake, as described above, is more restricted to the gullies and streamsides in this South-Eastern part of the island.

Blechnum palmiforme HEATH

The small tree-fern, *Blechnum palmiforme*, is widespread in the Fern Bush and Wet Heath. In the Fern Bush it dominates extensive areas of ground, often with no associated species except for epiphytes. The trunks of the *Blechnum* lie in a confused tangle, with their procumbent lower parts buried in the peat, and the upper parts, which are invariably covered in a thick layer of epiphytic ferns, producing a crown of stiff fronds up to 1m in diameter (Fig. 8), and often over 1.5m above the ground. There is generally no ground flora, and the few bryophytes of closed *Blechnum* heath are confined to the trunks of the tree-fern.

A community studied in detail (XXXII) lay on a slope of 30° to 50° at a height of 170m above the sea in The Glen. Fifty tree-ferns were here counted in an area of 35 sqm and the fronds from adjoining plants interlace about 2m above the ground, thus excluding much of the light from the peat surface where the plant cover is very sparse. Within a 7m quadrat, the following species were noted:

	field layer	ground layer	epiphytes
<i>Blechnum palmiforme</i>	95%	—	—
<i>Scirpus</i> sp.	+	+	—
<i>Empetrum rubrum</i>	—	+	—
<i>Nertera depressa</i>	—	+	+
<i>Brachythecium</i> sp.	—	++	—
<i>Elaphoglossum succisifolium</i>	—	+	+
<i>Gymnogramma cheilanthesoides</i>	—	+	—
<i>Hypnum elatum</i>	—	+	+
<i>Leptotheca gaudichaudii</i>	—	+	+
<i>Thuidium curvatum</i>	—	++	+
<i>Hymenophyllum pettatum</i>	—	—	70%
<i>H. aeruginosum</i>	—	—	++
<i>Adelanthus magellanicus</i>	—	—	++
<i>Bazzania skottsbergii</i>	—	—	++

A few fruit bodies of *Marasmius* sp. were collected from decaying *Empetrum* stems. In a drier area nearby where the *Blechnum palmiforme* cover is less dense, other ferns enter the community, notably: *Blechnum penna-marina*, *Elaphoglossum laurifolium*, *E. succisifolium*, *Histiopteris incisa*, *Asplenium obtusatum*.

On exposed ridges in the Fern Bush, *Blechnum palmiforme* is commonly associated with *Acaena sarmentosa*, which scrambles over the outspread fronds and the upper trunks. Epiphytes and ground flora in such communities are generally less abundant than in the pure *Blechnum palmiforme* heath, and the tree-fern is more stunted, the exposed trunk rarely exceeding 1m in length. Coverages within a 10-m strip along an exposed crest at 200m in The Glen (IX) were found to be:

	field layer	trunk epiphytes & ground layer
<i>Blechnum palmiforme</i>	40%	—
<i>Acena sarmentosa</i>	30%	—
<i>Phylica arborea</i>	+	—
<i>Elaphoglossum laurifolium</i>	5%	—
<i>Rumohra adiantiformis</i>	10%	—
<i>Carex thourarii</i>	+	—
<i>Asplenium alvaradense</i>	—	20%
<i>Hymenophyllum aeruginosum</i>		5%
<i>H. pettatum</i>		10%
<i>Brachythecium cf. rutabulum</i>		30%
<i>Adelanthus unciniformis</i>		+
<i>Bazzania skottsbergii</i>		+
<i>Drepanolejeunea tristaniana</i>		+
<i>Lepidoxia halleana</i>		+
<i>Lophocolea chiloensis</i>		+
<i>L. muricata</i>		+
<i>L. puccioana</i>		+
<i>L. wacei</i>		+
<i>Metzgeria multiforme</i>		++
<i>Plagiochila wacei</i>		+
<i>Pseudomarsipidium piliferum</i>		+



FIG. 8. *Blechnum palmiforme* dwarf tree-fern on the side of a steep gully in The Glen. The wet peat has slipped away from the rock, together with the overlying vegetation, revealing a clump of *Elaphoglossum succisifolium* below the climber. *Histiopteris incisa*, *Hypolepis rugosula* and *Scirpus* sp. associated with the *Blechnum palmiforme* to the left of the path; *Phylica* leaves in the right foreground.

Such communities are transitional to the *Blechnum palmiforme* heath found above the Fern Bush and Tussock Grassland formations, and described under Wet Heath below.

Phylica arborea BUSH

The heath-like microphyllous tree *Phylica arborea* forms dense thickets all over the broken ground and more sheltered parts of the Glens below 300 m. Scattered trees grow on exposed ridges and open slopes in the same zone, and amongst the Tussock Grassland of the western cliffs, but no *Phylica* was seen above a height of 450m above sea level. On Gough Island, as on Tristan da Cunha (Wace & Holdgate 1958), *Phylica arborea* has a procumbent habit, the trunks lying on or under the peat and sending up twisted branches to a height of about

5m (Fig. 12). Since *Phylica* is the only ecologically important tree on the island, and therefore has no competitors of the same life form, it produces a pure but irregular canopy wherever it dominates any community. *Sophora macnabiana*, the only other tree, is confined to two places in the *Sophora* Glen, where it dominates communities which are structurally similar to *Phylica* Bush.

Phylica bush is typically a 3-layered community. Where the canopy is thick, there is only a sparse understory, but in open *Phylica* bush, *Histiopteris incisa* and *Dryopteris aquilina* often form a dense layer beneath the trees up to 1m in height. A ground layer consisting of small ferns (notably *Asplenium alvaradense*) and bryophytes grows under thick *Phylica* canopy, where the understory is thinner. Epiphytes on the branches are very abundant: *Hymenophyllum* spp., *Asplenium alvaradense*, *Oncophorus fuegianus* and *Plagiochila wacei* are conspicuous near the ground; and *Macromitrium antarcticum*, *Metzgeria multiforme*, *Frullania lindenberghii*, and *Parmelia revoluta* on more exposed branches over 1m from the ground. *Phylica* has small hairy leaves borne in clusters at the ends of the branches, and there are no epiphyllous liverworts.

A typical patch of *Phylica* bush in The Glen at 90m above sea level (III) is illustrated diagrammatically in Figure 9. The main *Phylica* canopy, 3 to 4m high, is developed over a small horizontal terrace in a 20° slope. Probing revealed that the peat is more than 30 cm deep, but the surface is very uneven, with hummocks formed from the partially decayed trunks of *Blechnum palmiforme* beneath the litter. In the sampled area of 100 sq m the following species were found, with the indicated coverages in the 3 layers of the community:

	Tree 90%	Understory	Ground
<i>Phylica arborea</i>			
<i>Histiopteris incisa</i>		50%	
<i>Asplenium insulare</i>		10%	
<i>Dryopteris aquilina</i>		5%	
<i>Uncinia brevicaulis</i>		5%	
<i>Blechnum penna-marina</i>		++	
<i>Blechnum palmiforme</i>		++	
<i>Asplenium obtusatum</i>		+	
<i>Apium australe</i>		+	
<i>Elaphoglossum laurifolium</i>		+	
<i>E. succisifolium</i>		+	
<i>Scirpus</i> sp.		+	
<i>Vittaria vittarioides</i>		+	
<i>Asplenium alvaradense</i>			80%
<i>Nertera depressa</i>			+
<i>Hypnum elatum</i>			+
<i>Brachythecium subplicatum</i>			+
<i>Lophocolea monica</i>			+
<i>L. muricata</i>			+
<i>L. wacei</i>			+
<i>Telaranea nematodes</i>			+

The trunks of *Blechnum palmiforme*, and rotten *Phylica* wood lying on the ground are covered with a thick growth of *Hymenophyllum aeruginosum*. Epiphytes on the *Phylica* branches are very abundant. Those collected from this site were:

	less than 1 m above the ground	more than 1 m above the ground
<i>Asplenium alvaradense</i>	a.	+
<i>Hymenophyllum peltatum</i>	f.	o.
<i>Brachythecium cf. rutabulum</i>	o.	
<i>Hypnum elatum</i>	o.	
<i>Macromitrium antarcticum</i>		f.
<i>Calypogeia bidentula</i>	++	
<i>Drepanolejeunea araucariae</i>		
<i>chilensis</i>	++	+
<i>D. lancifolia</i>	+	
<i>D. tristaniana</i>	++	+
<i>Frullania lindenberghii</i>		++
<i>Jamesoniella oenops</i>	+	
<i>Lejeunea flava</i>		+
<i>Lepidozia halleana</i>	++	
<i>L. procumbens</i>	+	
<i>Leucolejeunea tristaniana</i>	+	
<i>Lophocolea humilis</i>	+	
<i>L. monoica</i>	+	
<i>L. submuricata</i>	+	
<i>L. wacei</i>	+	
<i>Metzgeria multiforme</i>	++	
<i>M. violacea</i>		++
<i>Microlejeunea ulicina</i>	+	
<i>Plagiochila wacei</i>	+	
<i>Telaranea nematodes</i>	+	
<i>Parmelia revoluta</i>		va.
<i>Parmelia</i> sp. indet.		
<i>Pseudocyphellaria aurata</i>		f.
<i>P. intricata</i>		f.
<i>P. cf. latifrons</i>		o.
<i>Usnea cf. rubingea</i>		o.

The lichens are confined to the upper parts of the branches, and are there very abundant. *Trentepohlia* sp. is frequently found on the *Phylica* bark in this region also.

The phytogeographically interesting species *Sophora macnabiana* was found in two places beside the stream in the Sophora Glen. The lower community at 100m above the sea near the uppermost reaches of a long straggling penguin rookery, was studied in detail to see whether any light could be thrown on the status of *Sophora* in the island, especially since some authors have assumed that it was introduced by man (Wilkins 1925, Good 1953 p. 117). The species present in an area 30m by 20m in a small gully South of the stream (XI) were found to be:

	Tree 60%	Understory	Ground
<i>Sophora macnabiana</i>			
<i>Histiopteris incisa</i>		35%	
* <i>Agrostis stolonifera</i>		15%	
<i>Dryopteris aquilina</i>		10%	
<i>Blechnum penna-marina</i>		10%	
<i>Uncinia brevicaulis</i>		5%	
<i>Ranunculus carolinii</i>		++	
<i>Thelypteris tomentosa</i>		++	
<i>Dryopteris paleacea</i>		+	
* <i>Rumex obtusifolius</i>		+	
<i>Carex insularis</i>		+	
<i>Vittaria vittarioides</i>		+	
<i>Asplenium obtusatum</i>		+	
<i>Brachythecium cf. rutabulum</i>			60%
<i>Asplenium alvaradense</i>			20%
<i>Hydrocotyle leucocephala</i>			++
<i>Nertera depressa</i>			+

The epiphytes are similar to those of *Phylica* bush. With the exception of the dominant species (which

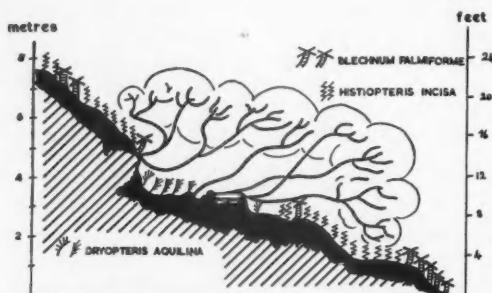


FIG. 9. Profile diagram of a *Phylica arborea* thicket in The Glen at 90m above sea level. Quadrat site III.

replaces *Phylica arborea*), and the species which are not native to the island (which are frequent in the nearby penguin rookeries), the structure and species-composition of the Sophora-dominated community are similar to those of *Phylica arborea* bush. A detailed exploration of all the Glens, and the Southern slopes, may reveal *Sophora* outside the Sophora Glen, but the tree is not an important constituent of the vegetation, and is best included under *Phylica arborea* bush in any classification of the vegetation types. There seems no reason to doubt that *Sophora macnabiana* is native to Gough Island (Wace, in preparation).

The 3-storied *Phylica* communities, as described from site III above, are typical of the relatively sheltered ground on deep peat in the Glens where there is probably a consistently high humidity. To the South of the island on the very broken ground below 100m the *Phylica* communities are of two types: those growing in the gullies which have a dense understory of ferns as in the Glen communities; and thickets in the more level areas having the same type of structure as the *Phylica* bush in the Glens, but in which *Apium australe*, *Asplenium obtusatum*, *Carex insularis* and *Spartina arundinacea* are the important understory species. These latter communities in which the flowering plants make up a substantial part of the understory are transitional to the small areas of *Phylica* bush amongst and above the tussock grasslands of the West coast, in which *Poa flabellata*, *Carex insularis* and *Asplenium obtusatum* are the most important components of the understory, and *Macromitrium antarcticum* and lichens the only epiphytes on the *Phylica* branches.

SERIAL STAGES LEADING TO FERN BUSH

Fern Bush is thickly developed upon peat which covers the steep sides of the Glens. In such places, strips of the peat with the plant communities growing upon them often slip away from the underlying rock down to the valley bottoms. All stages in the recolonisation of rock which has been bared by such peat-slips, up to the formation of mature Fern Bush, are found. Such seral communities were studied in two areas.

At 100m above the sea opposite Goncalo Alvarez in The Glen (VII), *Campylopus introflexus* and *Pohlia* sp. are the most important colonists of plant debris in the rock crevices of a 45° slope from which the peat has slipped away. Larger crevices, and hollows in the rock filled by peat from the previous Fern Bush cover, are colonised by:

<i>Scirpus sulcatus</i>	d.
<i>Poa flabellata</i>	o.
<i>Gnaphalium pyramidale</i>	f.
<i>Campylopus vesticaulis</i>	a., 1d.
<i>C. luscinalis</i>	o.

Patches which are kept moist by seepage from the surrounding Fern Bush peats support a dense growth of *Marchantia polymorpha*. *Empetrum rubrum* and **Holcus lanatus* which later colonise the *Scirpus*-dominated crevice communities by seed, form mats over the rock surface which are in turn invaded by seedlings of *Phylica arborea* and rhizomes of *Histiopteris incisa* from the surrounding Fern Bush communities.

A line of 6 quadrats (XII a-f), each 7m square and together forming a belt transect, was laid across another large peatslip area at a height of 110m on a slope of 35° in The Glen (Fig. 10).

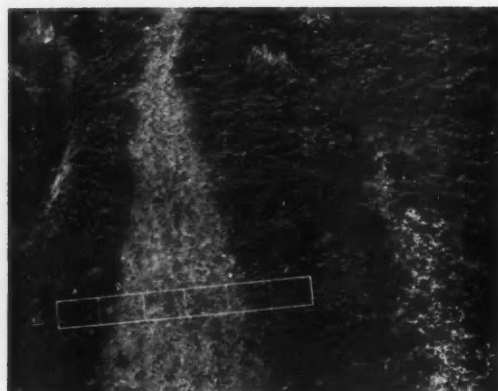


Fig. 10. Peatslip in The Glen fernbush, showing the site of the belt transect XII at 110m above sea level.

Recolonisation of this area had reached a later stage than that described above, and continuous cover had been formed over the central areas, largely by *Agrostis media* and **A. stolonifera*. The coverages of the principal species within the 6 quadrats are shown in Fig. 11.

The communities in this transect are of 3 types: i) Climax Fern Bush surrounding the peatslip area, dominated by *Phylica*, *Histiopteris*, and *Blechnum palmiforme* growing on peat about 1m deep, and with their usual associated species and epiphytes as previously described (XIIa & f) ii) Marginal strips dominated by a closed herbage about 0.7m tall, of **Holcus lanatus* and *Apium australe* on peat only about 15cm deep, and with a ground layer of almost pure *Brachythecium* cf. *rutabulum*, and containing also:

<i>Scirpus thourarsianus</i>	a.
<i>Hydrocotyle leucocephala</i>	f.
<i>Nertera depressa</i>	f.
<i>Carex insularis</i>	f.
<i>Deschampsia</i> sp.	r.

Both of the principal tussock-forming grasses (*Poa flabellata* & *Spartina arundinacea*) occurred sporadically outside the sample quadrats (XIIb & e) in this marginal area, which is invaded by rhizomes of *Histiopteris* and *Hypolepis rugosula* from the surrounding climax Fern Bush.

iii) A central area (XIIc & d) where the peat is less than 10cm deep, supporting a community dominated by *Agrostis media*, **A. stolonifera* and *Empetrum rubrum* which are associated with:

<i>*Holcus lanatus</i>	f.
<i>Blechnum penna-marina</i>	o.
<i>Gnaphalium pyramidale</i>	o.
<i>Carex thourarsii</i>	o.
<i>Lycopodium diaphanum</i>	o.
<i>Elaphoglossum laurifolium</i>	o.
<i>E. succisifolium</i>	o.
<i>Nertera depressa</i>	o.

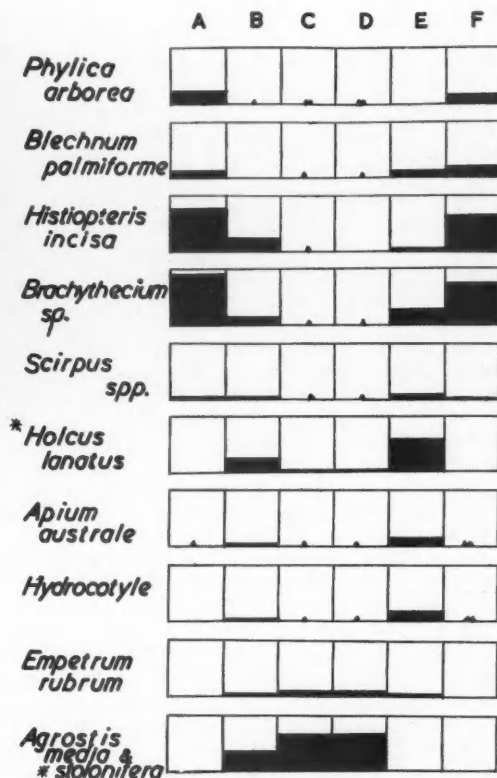


Fig. 11. Percentage coverages of the principal species within the 6 quadrats comprising the belt transect XII (see Figs. 10, 12). The totals for the outer quadrats exceed 100% because the cover within each layer of the community was noted.

and with sporadic young plants of *Phylica arborea* and *Blechnum palmiforme*. Bryophytes cover about 10% of the ground in this central area, and those collected were:

<i>Ditrichum strictum</i>	a.
<i>Jamesoniella grandiflora</i>	f.
<i>Polytrichum juniperinum</i>	f.
<i>Philonotis tenuis</i>	f.
<i>Polytrichadelphus magellanicus</i>	o.
<i>Polytrichum gracile</i>	o.
<i>Sphagnum magellanicum</i>	o.
<i>S. fimbriatum</i>	o.
<i>Breutelia cf. plicata</i>	o.
<i>Brachythecium subplicatum</i>	r.
<i>Campylopus introflexus</i>	r.
<i>Drepanocladus uncinatus</i>	r.

together with the smaller liverworts: *Isotachis specgazziana*, *Lejeunea longicollis*, *Lepidozia halleanta*, *L. procumbens*, *Lophocolea monica*, *L. puccioana*, *L. textilis*, *Metzgeria multiforme*, *Mylia chiloscypoides*, *M. ligulata*, *M. repens*. Figure 12 illustrates these 3 types of community involved in the recolonisation of this peatslip.



FIG. 12. View across the top of the peatslip shown in Fig. 10, illustrating the principal communities involved in the seral stages of recolonisation. *Agrostis* spp., *Empetrum rubrum* and bryophytes on thin peat in the foreground; *Apium australe*, *Deschampsia* sp. and *Holcus lanatus* in the marginal strip; *Histiopteris incisa*, *Blechnum palmiforme* and *Phylica arborea* of mature fernbush in the background. The mean angle of slope is c. 35° from the horizontal.

Flowering plants are seen to be far more important in the seral stages of Fern Bush than in the climax vegetation itself, where (apart from *Phylica* and *Apium*) they may be almost totally absent over considerable areas. As in the climax Fern Bush, a greater degree of exposure is associated with a decline in the importance of pteridophytes in the community. All the flowering plants mentioned as colonists of peatslips undoubtedly spread into these areas mainly by seed, but despite an abundance of open habitats in Fern Bush and

elsewhere due to recurrent peatslip on steep slopes, only *Gnaphalium pyramidale* amongst the native species has the therophyte life form generally associated with the exploiters of such habitats (Wace, in prep.). Although some sporelings of *Blechnum palmiforme* and *Histiopteris incisa* colonise peatslip areas, most of the ferns spread onto such areas by marginal vegetative growth from the surrounding Fern Bush communities.

CYCLIC AUTOGENIC CHANGES IN FERN BUSH

The three associations comprising the Fern Bush are not distributed entirely at random. In the Glens, *Blechnum palmiforme* is generally dominant on very broken ground without deep peat deposits; *Histiopteris* generally dominates the gentler and more uniform slopes where deep peat accumulates; and the proportion of *Phylica* is greatest on the very steep eastward-facing slopes. The distribution of these three communities on slopes of various aspect and steepness in The Glen is shown in Fig. 13.

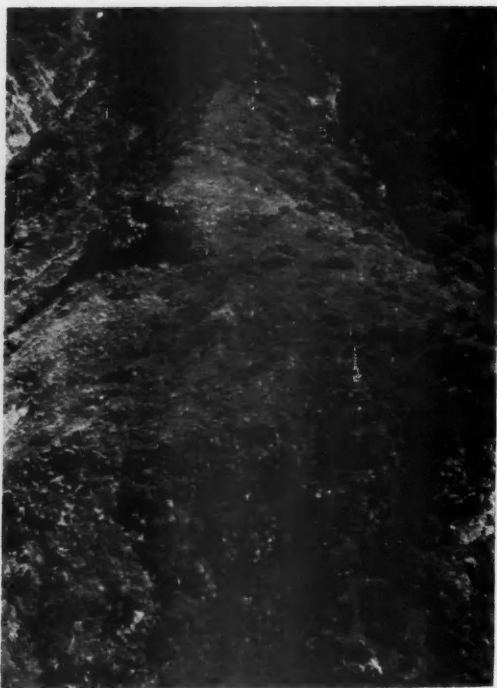


FIG. 13. Undisturbed fernbush on the North-facing slope of The Glen, opposite the peatslip shown in Fig. 10. *Histiopteris incisa* predominates on the gentler slopes, and *Phylica arborea* on the steeper sides of the ridges. *Blechnum palmiforme* is more uniformly scattered.

Such observations as these suggest a polyclimax type of vegetation, where the distribution of the various dominants is determined by static environmental preferences. That this is not the entire explanation, and that some cyclic autogenic processes

are operating, at least on the steeply-sloping ground in the Glens, is suggested by the following facts:

- Although closed *Histiopteris* communities on peat of over 1m in depth very rarely contain seedlings of *Phylica* or sporelings of *Blechnum palmiforme*, the trunks of both these plants were found in the peat beneath all the *Histiopteris* communities that were investigated.
- Phylica*, and to a lesser extent *Blechnum palmiforme*, colonise peatslip areas by seed and spore in advance of the vegetatively spreading *Histiopteris*.
- Where *Phylica* thickets and areas of closed *Blechnum palmiforme* are surrounded by *Histiopteris*-dominated communities, the peat under the *Histiopteris* is deeper than under the others.

Histiopteris renews all its fronds annually, and the depth of peat produced every year by the pure *Histiopteris* communities must be considerable. This peat is moist and loosely-packed on top, and the *Histiopteris* rhizomes which hold it together are brittle, and confined to the top ½m. They can scarcely be effective in anchoring a deep accumulation of peat which is saturated with water, to the underlying rock.

It therefore seems that *Histiopteris* smothers both *Phylica* and *Blechnum palmiforme* by its rate of peat accumulation, and then builds up communities which become unstable on slopes of over about 30°, due to the accumulation of thick peat which is not anchored effectively to the rock, and these

accumulations periodically give rise to the peatslips already described. *Phylica* can maintain closed communities on slopes of up to 70° from the horizontal by its rooting into the rock fissures and the downhill method of growth of its procumbent trunks, and *Blechnum palmiforme* is to a lesser extent capable of maintaining a closed community on the small areas of steep slope in very broken gullied ground.

In its simplest form, the sequence of communities involved in the build-up and re-colonisation of peatslips in the Gough Island Glens on slopes of about 30° to 45° is shown in Figure 14. The Glen peatslips are of great importance in allowing the entry of *Phylica* and *Blechnum palmiforme* into what would otherwise become closed *Histiopteris* communities. The Fern Bush vegetation in the Glens of Gough Island is thus seen to be a mosaic whose components are in a state of dynamic equilibrium similar in principle to those described from Britain by Watt (1947). Similar but less striking cyclic processes depending upon peat buildup on steep slopes are seen in Tussock Grassland and Wet Heath vegetation on Gough Island. An important factor contributing to the instability of the peat in all the Gough communities is the disruption caused by burrowing activities of the millions of ground-nesting sea birds (Swales, in preparation).

Areas of Fern Bush on flatter ground, where the gradients do not exceed 30° from the horizontal, would be expected from the above-described theory to be dominated mainly by *Histiopteris* communities. The only extensive area of gently sloping lowland, in the South of the island bears a mixture of *Phylica* and *Blechnum palmiforme* communities, but *Histiopteris* is less important, and replaced by the *Asplenium obtusatum*, *Rumohra adiantiformis*, *Empetrum rubrum* and *Carex insularis* communities previously mentioned. It is possible that *Histiopteris* requires a more constant humidity, or relative freedom from exposure to heavily salt-laden winds, which conditions obtain in the East and North coast Glens but not in the low lying ground to the South of the island.

Examples of humus build-up and landslide which are entirely similar to the Gough Island peatslips have been described from Oahu and Hawaii by Wentworth (1943). In Oahu, 80% of the slides recorded occur on slopes of between 42° and 48° from the horizontal, and the thickness of the dislodged material is generally less than 1m, the slides tending to recur in the same places during periods of heavy rain. In Gough Island, where the physiographic conditions are very similar to those on Oahu, it is probable that peatslips occur under similar circumstances, although greater depths of peat undoubtedly give rise to slides on slopes as little as 30° from the horizontal in many cases. The "oversteepening" of the valley sides and the formation of "knife-edge" ridges recorded from Oahu are also clearly evident on Gough Island (Wentworth 1928).

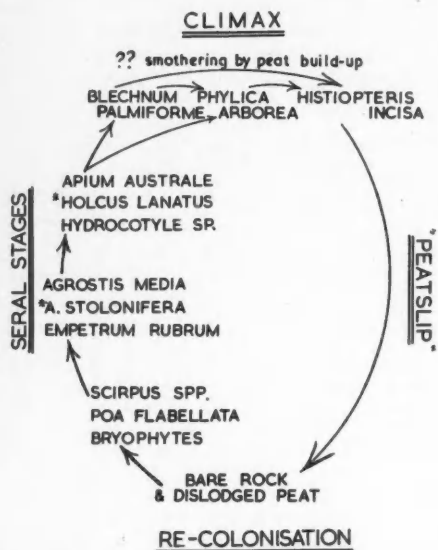


FIG. 14. Diagram illustrating the sequence of communities involved in the autogenic peatslip cycle in The Glen fernbush on slopes of 30° to 45° from the horizontal.

Frequent "bog slides" are also noted from the Auckland Islands by Aston (1909), but the Gough Island peatslips are not strictly comparable to the "bog bursts" described from Ireland and elsewhere by Preager & Sollas (1897) and Delap, Farrington, Preager & Smith (1932). It is clear, however, that the Gough Island peatslips are only a particularly rapid-cycling and spectacular example of a retrogressive process common to all peat-forming communities (Osvald 1949, Gorham 1957).

THE HABITAT FACTORS AND GEOGRAPHICAL RELATIONS OF FERN BUSH

Tussock Grassland and Fern Bush are complementary in their distribution on Gough Island. Below about 300m the Tussock covers the slopes fully exposed to the prevailing westerly winds, and the Fern Bush the sheltered Glens, while the Southern slopes have some species from both the formations. Neither *Blechnum palmiforme* nor *Histiopteris incisa* grow in places exposed to much salt spray, and Fern Bush is only fully developed in relatively sheltered and humid situations away from the shores.

The Gough Island Fern Bush is very similar to the *Phyllea* bush on Tristan da Cunha (Wace & Holdgate 1958). It differs principally in the greater importance of *Histiopteris incisa* on Gough, which is largely replaced by *Dryopteris aquilina* on Tristan. This difference is probably associated with the considerably wetter climate of Gough, for the epiphytes are less abundant in the Tristan Fern Bush community. Apart from these minor differences, the communities on the two islands resemble one another closely, both structurally and floristically.

Fern Bush is also structurally similar to the upper arboreal vegetation of many tropical mountains (Troll 1958), and its structural relationships to microphyll thicket vegetation on other islands and volcanic mountains have been discussed by Wace & Holdgate (1958) and Wace (1960). The general points of resemblance in all these communities are the dominance of one, or a small number of species of straggling heath-like microphyllous evergreen trees without a continuous canopy, the importance of ferns in the field layer and understory, and the abundance of cryptogamic epiphytes.

There are no structural resemblances between the Fern Bush and *Phyllea* bush of the Gough-Tristan group, and the evergreen *Nothofagus* forests of Fuegia, Western South America, and New Zealand.

WET HEATH

Between 300 and 600m above sea level, there is a zone of Wet Heath vegetation dominated by stunted *Blechnum palmiforme*, *Empetrum rubrum*, and various grasses and sedges. This intermediate zone borders on all the other vegetational formations in the island, containing elements from them all, and is therefore the most difficult formation to typify. Three associations are recognised.

Blechnum palmiforme HEATH

The small tree-fern extends above the upper limits of Fern Bush to form a zone in which it dominates parts of the Glens and the southern slopes up to a height of about 375m. Close to the upper limits of the Fern Bush, the patches of *Blechnum palmiforme* heath are essentially similar to those described from the Fern Bush itself, except that the trunks are generally less than 1m tall, with fewer epiphytes, and the communities are more open, with a number of associated species.

Open *Blechnum palmiforme* heath in The Glen at a height of 350m above sea level on the South-East side (i.e. the lee side) of an exposed ridge contained the following species within a 7m quadrat (XIII, Fig. 15):



FIG. 15. Rhacomitrium—Empetrum moor (left), and open *Blechnum palmiforme* heath (right) at 350m above sea level on the flanks of a ridge in The Glen. The dwarf tree-fern is absent from the exposed north-western slope, but dominates the vegetation on the more sheltered south-east side of the ridge.

	field layer	ground layer
<i>Blechnum palmiforme</i>	60%	
<i>Empetrum rubrum</i>	30%	10%
<i>Apium australe</i>	++	
<i>Uncinia compacta</i>	+	
<i>Spartina arundinacea</i>	+	
<i>Deschampsia</i> sp.	+	
<i>Scirpus</i> sp.	+	5%
<i>Elaphoglossum laurifolium</i>		10%
<i>E. succisifolium</i>		
<i>Blechnum penna-marina</i>		+
<i>Lagenophora nudicaulis</i>		+
<i>Nertera depressa</i>		+
<i>Rhacomitrium lanuginosum</i>		25%
<i>Dicranoloma impenens</i>		20%
<i>D. hartioides</i>		10%
<i>Ptychomnion densifolium</i>		15%
<i>Lepyrodion alaris</i>		++

Hymenophyllum peltatum, *Bazzania skottsbergii* and *Jamesoniella colorata* are conspicuous as epiphytes on the *Blechnum* trunks, and the following liverworts were also collected from this habitat, and from the ground: *Adelanthus magellanicus*, *A. unciniformis*, *Aphanolejeunea microscopica*, *Blepharidophyllum densifolium*, *Isotachis fragilis*, *Jamesoniella oenops*,

Lepicolea ochroleuca, *Lepidozia procumbens*, *L. sadlensis*, *Lophocolea humilis*, *L. monoica*, *Plagiochila vacei*, *Trichocolea verticillata*.

Above the Tussock Grass communities of the West coast, on the more level ground at the top of the cliffs, *Blechnum palmiforme* grows in thick stands reminiscent of a pineapple plantation, with stunted trunks often overgrown by *Acaena sarmentosa*. At 330m above sea level at the top of the cliffs overlooking Saddle Island, the following species were recorded from a 10m quadrat (LXV):

<i>Blechnum palmiforme</i>	65%
<i>Acaena sarmentosa</i>	20%
<i>Blechnum penna-marina</i>	++
<i>Elaphoglossum laurifolium</i>	+
<i>E. succisifolium</i>	++
<i>Empetrum rubrum</i>	+
<i>Scirpus</i> sp.	+

Blechnum penna-marina also grows as an epiphyte, together with *Asplenium alvaradense* and *Hymenophyllum peltatum*, on the trunks of the tree-ferns. The *Blechnum palmiforme* fronds in these cliff-top communities are much blackened (possibly because of salt spray) and the plants dwarfed and stunted in comparison with the same species at the same altitude in the Eastern Glens. Tussock grasses occur here and there in rocky hollows amongst the tree-ferns, and *Phylla* (here at the upper limit of its altitudinal range) forms occasional low stunted clumps in the sheltered gullies.

Empetrum rubrum HEATH

Between about 375 and 500m above sea level, but extending higher in sheltered places, *Empetrum rubrum* dominates 2 distinct types of community above the *Blechnum palmiforme* heath. A prostrate growth form of *Empetrum* with many of the procumbent shoots severely fasciated, forms mats over *Sphagnum* spp. on wet peat and a close-growing compact type forms deep springy cushions in wind-swept areas which are well drained.

A *Sphagnum*-*Empetrum* community at the foot of the Hag's Tooth 430m above sea level was studied in detail. A 10-m quadrat (LV) contained the following species:

<i>Empetrum rubrum</i>	35%
<i>Sphagnum</i> sp.	20%
<i>Blechnum palmiforme</i>	15%
<i>Deschampsia</i> sp.	10%
<i>Blechnum penna-marina</i>	5%
<i>Nertera depressa</i>	++
<i>Agrostis</i> sp.	10%
<i>Uncinia compacta</i>	++
<i>Elaphoglossum succisifolium</i>	++
<i>Lagenophora nudicaulis</i>	++
<i>Apium australe</i>	++
<i>Carex thouratii</i>	+
<i>Acaena sarmentosa</i>	+
<i>Racomitrium lanuginosum</i>	++
<i>R. loriforme</i>	+
<i>Lepicolea ochroleuca</i>	++
<i>Ptychomnion densifolium</i>	++
<i>Dicranoloma</i> sp.	+

There were also a number of liverworts, which were not collected. The peat beneath this community con-

sisted principally of the remains of *Sphagnum* together with numerous stems of *Empetrum*, and some trunk fragments of *Blechnum palmiforme*. Such communities as this, although very wet, contain no standing water between the irregular mounds of *Sphagnum*.

The cushion type of *Empetrum* heath communities are widespread on the western side of the island, and surrounding the valley bogs in Gonydale and Albatross Plain. The *Empetrum* forms a compact layer up to 25cm deep, and is often associated with *Racomitrium lanuginosum* (more abundant at greater heights) and other bryophytes. Associated flowering plants are generally quite unimportant in these *Empetrum* cushions, although *Deschampsia* sp., *Spartina arundinacea* and *Apium australe* may all be abundant locally, and *Tetroncium magellanicum* present in damp hollows. Two 10-m quadrats yielded the following lists of species in these communities:

	XXVIII (S-W Gonydale)	LXVI (Rockhopper Point cliff- top)
<i>Empetrum rubrum</i>	60%	5%
<i>Spartina arundinacea</i>		50%
<i>Deschampsia</i> sp.		15%
<i>Tetroncium magellanicum</i>	10%	15%
<i>Blechnum palmiforme</i>		5%
<i>Apium australe</i>	+	5%
<i>Scirpus</i> sp.	5%	+
<i>Blechnum penna-marina</i>	++	++
<i>Elaphoglossum succisifolium</i>		++
<i>Racomitrium lanuginosum</i>	15%	
<i>Ptychomnion densifolium</i>	++	
<i>Dicranoloma imponens</i>	+	
<i>Rhacocarpus humboldtii</i>	+	
<i>Polytrichum juniperinum</i>	+	
<i>Breutelia</i> cf. <i>plicata</i>	+	
<i>Lepicolea ochroleuca</i>	+	

Epiphytic bryophytes are absent from the exposed cliff top community, but *Asplenium alvaradense* grows on some of the *Blechnum palmiforme* trunks.

Another area that was studied supported a community in which *Empetrum* was the most important species, but associates were more frequent, and epiphytes on the *Empetrum* stems very abundant. This very mixed type of Wet Heath, where there is no clear dominant and there are numerous bryophytes is typical of much of the vegetation between the Fern Bush and the montane communities, in moderately sheltered conditions and poor drainage. The community studied was on the South-East flank of Green Hill, on wet peat about 1.5m deep, and consisted of a loose springy mat of *Empetrum* growing amongst moss hummocks into which the tufted flowering plant associates were rooted. A 10-m quadrat (XXV) contained the following species:

<i>Empetrum rubrum</i>	25%
<i>Scirpus</i> sp.	20%
<i>Apium australe</i>	10%
<i>Blechnum palmiforme</i>	10%
<i>B. penna-marina</i>	5%
<i>Deschampsia</i> sp.	++

<i>Dryopteris aquilina</i>	+
<i>Lagenophora nudicaulis</i>	+
<i>Hydrocotyle leucocephala</i>	+
<i>Acaena sarmentosa</i>	+
<i>Carex thourarii</i>	+
<i>Elaphoglossum laurifolium</i>	+
<i>E. succisifolium</i>	+
<i>Asplenium alvaradense</i>	+
<i>Drepanocladus uncinatus</i>	++
<i>Ptychomnion densifolium</i>	5%
<i>Rhacomitrium lanuginosum</i>	++
<i>R. loriforme</i>	++
<i>Brachythecium subplicatum</i>	+
<i>Breutelia cf. plicata</i>	++
<i>Dicranum sp.</i>	++
<i>Lepyrodon alaris</i>	+
<i>Thuidium curvatum</i>	+

A small pool in one corner of the quadrat contained a little *Callitriche christensenii*. Communities of this type are intermediate between the Empetrum heath described earlier in this section, and the mixed grass-and-sedge heaths described below.

GRASS AND SEDGE HEATH

Communities dominated by a mixture of *Carex* spp., *Uncinia* spp., *Deschampsia* sp., *Agrostis media*, and *Apium australe* are common on broken ground and on flushed peat above the altitudinal limits of Fern Bush and Tussock Grassland. These communities are particularly characteristic of the upper 150m of the Eastern and Northern glens, under the scarp of the Tarn Moss Plateau, but they also occur on the margins of all the big peat bogs and in the more sheltered gullies which drain the central peaks, including the floor of the broken crater of Edinburgh Peak. The grasses and sedges have a tufted habit, growing in a loose hummocky carpet of bryophytes, principally *Lepicolea ochroleuca* and *Breutelia cf. plicata* and *Dicranoloma* spp. Sphagnum is not an important constituent of this type of community, although Sphagnum hummocks occur where there is no flushing from the ground water. The peat upon which these communities grow is not generally more than 20cm deep, and is loose-packed and unstable on the steep slopes, slipping away readily when trodden on.

Three 10-m quadrats amongst grass-sedge heaths yielded the following lists of species:

	LVI	XXXVIII	LXII
	West end	Crater	West slopes
	The Glen	Edinburgh	Edinburgh
	600m.	760m.	725m.
<i>Deschampsia</i> sp.	30%	20%	25%
<i>Apium australe</i>	5%	10%	10%
<i>Ranunculus caroli</i>	++	10%	10%
<i>Scirpus</i> sp.	+	15%	10%
<i>Glyceria</i> sp.	+	20%	5%
<i>Blechnum penna-marina</i>	20%	+	5%
<i>Hydrocotyle leucocephala</i>	+	++	
<i>Cardamine glacialis</i>		+	+
<i>Carex thourarii</i>	10%		+
<i>Agrostis carmichaelii</i>			15%
<i>A. media</i>	10%		
<i>Uncinia compacta</i>	++		++
<i>Nertera depressa</i>	+		+
<i>Acaena stangii</i>	10%	+	
<i>Empetrum rubrum</i>	5%		

<i>Dryopteris aquilina</i>			+
<i>Hymenophyllum pettatum</i>			+
Bryophytes (collectively)	10%	15%	20%
<i>Brachythecium subplicatum</i>	+	++	
<i>Dicranoloma</i> sp.	++		++
<i>Ptychomnion densifolium</i>	++		5%
<i>Bryum</i> sp.	+	++	
<i>Sphagnum fimbriatum</i>	+	++	
<i>Breutelia cf. speciosa</i>	++	++	

The following liverworts were collected from LXII: *Anastrophyllum crebrifolium*, *Lepidozia procumbens*, *Riccardia savatieri*, *Syzugiella tristiana*. Communities of this type are similar to some dominated by Cyperaceae found on re-distributed peat on the margins of the bog streams, but these latter communities are usually dominated by *Carex inularis*. They are described below under the Peat Bogs.

THE HABITAT FACTORS AND GEOGRAPHICAL RELATIONSHIPS OF WET HEATH COMMUNITIES

The factors controlling the distribution of the Wet Heath communities on Gough Island are less easy to understand than those which control the distribution of the other formations. It seems that Wet Heath is developed in all areas above the altitudinal limit of Fern Bush and Tussock Grassland where some peat accumulation is possible, but where there is no substantial hindrance to water runoff.

The *Blechnum palmiforme* heath is simply an upward extension of the same community in the Fern Bush, but is only found at the lower limits of the Wet Heath zone where its trunk growth can compete with the rate of peat formation of the surrounding plants: above about 375m the trunk becomes totally immersed in the peat and the fronds are borne on the peat surface. Neither degree of exposure nor waterlogging of the peat seem to limit the Empetrum- or *Blechnum palmiforme*-dominated communities, whereas the grass-sedge heaths are more restricted to moderately sheltered ground on the shallower peat, or amongst screes. None of the wet heath communities is obviously affected by snow-lie, but exposure is certainly one of the most important factors controlling the distribution of the formation as a whole, and the different communities within it.

Structurally, the upper communities of the Gough Island wet heaths resemble other temperate oceanic montane communities. A vegetation of creeping ericoid undershrubs, tufted grasses and sedges and bryophyte (often Sphagnum) hummocks, is typical of much of the British uplands (Pearsall 1950). As in the West European heath formation, the Gough heath is "a climatic formation on exposed coasts and on exposed mountain slopes between 300 and 600m., . . . In situations where the wind factor is definitely inimical to tree growth. . ." (Tansley 1939). The Gough formation is also equivalent to the Low Alpine zone of the Scottish and Norwegian mountains, recognised by Poore & Me-

Vean (1957), with the important exceptions that there are no equivalent life forms in the Gough heaths to the juniper or dwarf willow and birch of the European communities, and no equivalent in Europe to the dwarf tree-ferns of Gough.

The Gough Island wet heaths are both structurally and floristically similar to the Magellanic moorland of SW Chile (Godley 1960), and the Falkland Island heaths (Skottsberg 1913), which are developed in exposed situations with similar oceanic climates, but the Gough communities lack the cushion-forming flowering plants which play an important part in the continental peat-forming associations. The dwarf tree-fern life form of the Gough wet heaths is reminiscent of the high tropical mountains (Troll 1958), and it also occurs in the oceanic wet heaths of the New Zealand shelf islands (*Polystichum vestitum*, *Blechnum capense*, *B. durum*) and Masafuera in the Juan Fernandez group (*Blechnum cycadifolium*, *Lophosoria quadripinnata*).

MOORLAND, FELDMARK, AND MONTANE ROCK COMMUNITIES

Wet Heath vegetation can develop up to the highest points on Gough Island, where there is some shelter from wind, and where peat can accumulate; but most of the ground above 600m is exposed and windswept, and bears a montane moorland vegetation on thin mineral soils, verging in places to feldmark and bare rock.

RHACOMITRIUM—EMPETRUM MOORLAND

On windswept slopes above the Wet Heath, where the peat is only a few centimetres thick, *Empetrum rubrum* adopts a very straggling and close-growing habit, and does not form continuous mats or cushions as it does lower down. It is associated with *Rhacomitrium lanuginosum*, which grows amongst the woody *Empetrum* shoots and forms hummocks above them.

A community at 630m on the South-West face of Mount Rowett is exposed to the prevailing winds, and the mountainside is cut up by numerous shallow gullies filled with rocks and all more or less covered by thin peat which is overgrown by straggling *Empetrum* and hummocks of *Rhacomitrium lanuginosum*. A 10-m quadrat (XVI) in this area yielded:

<i>Empetrum rubrum</i>	30%
<i>Acaena stangii</i>	15%
<i>Agrostis carmichaelii</i>	10%
<i>Apium australe</i>	++
<i>Carex thouarsii</i>	+
<i>Blechnum penna-marina</i>	10%
<i>Deschampsia</i> sp.	5%
<i>Grammitis billardieri</i>	+
<i>Hydrocotyle leucocephala</i>	+
<i>Lagenophora nudicaulis</i>	++
<i>Lycopodium magellanicum</i>	++
<i>L. saururus</i>	+
<i>Nertera depressa</i>	+
<i>Ophioglossum opacum</i>	+
<i>Rostkovia triatanensis</i>	+
<i>Rumohra adiantiformis</i>	+
<i>Scirpus</i> sp.	+
<i>Rhacomitrium lanuginosum</i>	20%

Wet hollows between the rocks are filled with bryophytes, notably *Lepicolea ochroleuca* and *Jamesoniella grandiflora*, and the exposed rock surfaces bear tufts of *Andraea loricata*. This type of *Rhacomitrium*—*Empetrum* community is most abundant on the rough ground above 600m on the Western sides of the mountains: at the same heights on the Eastern sides it is generally replaced by the grass and sedge heaths already described.

Rhacomitrium lanuginosum is also an important associate of *Empetrum*, dominating some communities below 600m, as on the tops of the convex mounds of deep peat in the Gonydale valley bog (quadrat XXI—see below). Lower still, at a height of 350m just above the upper limit of Fern Bush, on the North-West (exposed) side of a ridge in The Glen, wind-cut *Empetrum* and *Rhacomitrium lanuginosum* overlie a wet peat 15cm deep, with low hummocks of bryophytes. The list of species recorded from a 7-m quadrat (XIV) was:

<i>Rhacomitrium lanuginosum</i>	30%
<i>Empetrum rubrum</i>	25%
<i>Agrostis media</i>	10%
<i>Scirpus</i> sp.	5%
<i>Blechnum penna-marina</i>	5%
<i>Uncinia brevicaulis</i>	++
<i>Lagenophora nudicaulis</i>	++
<i>Carex thouarsii</i>	+
<i>Spartina arundinacea</i>	+
<i>Lycopodium saururus</i>	+
<i>L. magellanicum</i>	+
<i>Deschampsia</i> sp.	+
<i>Nertera depressa</i>	+
<i>Gymnogramma cheilanthesoides</i>	+
<i>Dicranoloma imponens</i>	10%
<i>Thysanomitrium richardii</i>	5%
<i>Rhacocarpus humboldtii</i>	+
<i>Campylopus vesticaulis</i>	+
<i>Dicranoloma harti</i>	+
<i>Breutelia</i> cf. <i>plicata</i>	+
<i>Bazzania skottsbergii</i>	++
<i>Herberta oldfieldianum</i>	+
<i>Strepsilejeunea gayana</i>	+

This quadrat, and quadrat XIII bearing *Blechnum palmiforme* heath, lay on either side of a sharp South-West to North-East ridge (Fig. 15), and the contrast in their vegetation types illustrates the prime importance of aspect and exposure as determining factors. Although the most extensive areas of *Rhacomitrium*—*Empetrum* heath are found above 600m, the community is developed at much lower altitudes in very exposed areas.

Agrostis carmichaelii MOORLAND

Agrostis carmichaelii is a very abundant plant in all upland communities, except the plateau bogs. Above about 600m it dominates extensive areas of thin and often wind-eroding peat and shallow mineral soil on the flanks of the mountains, being replaced by Feldmark and rock in the most exposed situations. *Agrostis carmichaelii* and *Scirpus* sp. are the most important vascular plants, forming small tussocks up to 15cm high in a sodden surface layer of bryophytes, notably *Thysanomitrium richardii*, *Rhacocarpus humboldtii*, *Jamesoniella* spp., and

smaller liverworts. *Sphagnum* spp. are absent from these shallow windswept peat-and-mineral soils.

Two rather similar 10-m quadrats to the East of Green Hill at about 480m were studied. The peat here varies in depth from 15 to 50cm, and is shallowly terraced, with the flowering plants forming low hummocks and fronting the terrace steps, and the bryophytes on the flatter tops, often submerged in water. Drainage is entirely by surface runoff over the terraces, which contour the gentle (10°) slopes. The species coverages for these 2 quadrats were:

	XV	XXVII
<i>Agrostis carmichaelii</i>	20%	35%
<i>Scirpus thourarsianus</i>	10%	25%
<i>Carex thourarsii</i>	5%	++
<i>Ucinia compacta</i>	5%	++
<i>Lycopodium magellanicum</i>		5%
<i>L. saururus</i>	++	+
<i>Nertera depressa</i>	++	+
<i>Lagenophora nudicaulis</i>		+
<i>Deschampsia</i> sp.	++	
<i>Rostkovia tristanensis</i>		++
<i>Apium australe</i>	+	+
<i>Gymnogramma cheilanthesoides</i>	+	
<i>Blechnum penna-marina</i>	+	
<i>Thysanomitrium richardii</i>	15%	10%
<i>Rhacocarpus humboldtii</i>	10%	+
<i>Dicranoloma</i> sp.	+	++
Hepaticae (collectively)	25%	20%

The following hepaticae were collected from XV: *Adelanthus unciiformis*, *Drepanolejeunea tristaniana*, *Harpocladium minimum*, *Jamesoniella colorata*, *Lepicolea ochroleuca*, *Lepidozia humilis*, *Strepsilejeunea gayana*. Blanket peat communities of this type, in which the peat is permanently saturated with water, merge into the plateau bog vegetation described later, in which the water table is permanently at or just above the surface. *Sphagnum* spp. are generally unimportant in all these communities.

On the higher slopes of the mountains, very small plants of *Agrostis carmichaelii* cover a higher proportion of the ground than on the wet peaty communities described previously. The stunted tussocks, 5 to 10cm high may attain up to 80% cover on a raw humus and coarse rock fragment soil a few centimetres thick. Two 10m quadrats in such communities yielded the following lists of species:

	XXXV South face Nigel's Cap	XXXVI N-E face Edinburgh Pk.
<i>Agrostis carmichaelii</i>	40%	50%
<i>Apium australe</i>	10%	+
<i>Hydrocotyle leucocephala</i>	10%	
<i>Acaena stangii</i>	10%	
<i>Nertera depressa</i>		5%
<i>Deschampsia</i> sp.	5%	+
<i>Blechnum penna-marina</i>	++	5%
<i>Ucinia compacta</i>	++	
<i>U. brevicaulis</i>		+
<i>Ophioglossum opacum</i>	+	++
<i>Lycopodium magellanicum</i>		++
<i>L. saururus</i>		+
<i>Grammitis billardieri</i>	+	+
<i>Scirpus</i> sp.	+	++
<i>Lagenophora nudicaulis</i>		++
<i>Ranunculus caroli</i>	+	+
<i>Rostkovia tristanensis</i>		+

<i>Empetrum rubrum</i>		+
<i>Gnaphalium pyramidale</i>	+	
<i>Carex thourarsii</i>		+
<i>Rhacocarpus humboldtii</i>		15%
<i>Thysanomitrium richardii</i>		5%
<i>Andraea loricata</i>		5%
<i>Rhacomitrium lanuginosum</i>	++	
<i>R. loriforme</i>	+	+
<i>Lepicolea ochroleuca</i>		++
<i>Dicranoloma</i> sp.	+	+
<i>Psilopilum</i> sp.	+	+
<i>Breutelia</i> cf. <i>plicata</i>	++	
<i>Jamesoniella</i> spp.		++
<i>Symphogyna crassifrons</i>		+

About 15% of the quadrat on Nigel's Cap was occupied by protruding rock and stones, on which *Leicidia* sp. was very abundant. The lichens *Stereocaulon implexum* and *Placidopsis parallina* were also collected from this quadrat.

FELDMARK

In the moorland communities just described, flowering plants cover more than half the ground, but in the most exposed areas on the crests of the mountain ridges and the tops of the highest peaks, the rock is partially covered by a thin crust of bryophytes into which a few flowering plants root. Flakes of rock and grit are mixed with the thin peat, which usually shows signs of severe wind erosion. A very common effect produced by wind erosion on the Western side of exposed mountain ridges, shows dark coloured feldmark bryophytes contrasting markedly with the lighter *Agrostis* moorland on the lee side.

A 10-m quadrat (XXXI) on an exposed ridge at the head of The Glen at a height of 570m above sea level contained the following species:

<i>Agrostis carmichaelii</i>	20%
<i>Nertera depressa</i>	++
<i>Lycopodium magellanicum</i>	++
<i>Empetrum rubrum</i>	++
<i>Carex thourarsii</i>	+
<i>Ucinia brevicaulis</i>	+
<i>Lycopodium saururus</i>	+
<i>Lagenophora nudicaulis</i>	+
<i>Rhacocarpus humboldtii</i>	10%
<i>Thysanomitrium richardii</i>	5%
<i>Andraea loricata</i>	+
<i>Dicranoloma</i> sp.	+
(?) <i>Ditrichum</i> sp.	+
Hepaticae (collectively)	50%
<i>Aphanolejeunea microscopica</i>	
<i>Isotachis spegazziana</i>	
<i>Jamesoniella colorata</i>	
<i>J. grandiflora</i>	
<i>J. oenops</i>	
<i>Lepidozia saddlensis</i>	
<i>Symphogyna crassifrons</i>	

Stereocaulon implexum occurs sporadically, and becomes increasingly important at higher altitudes, and *Leceidea* sp. encrusts the exposed rock and stones which occupy about 10% of this quadrat. A close-up view of a part of this quadrat is shown in Fig. 16.

Vegetation of this type is typical of the crests of the ridges dividing the North and East coast glens, the long ridge connecting the various summits of



FIG. 16. Feldmark peat on an exposed mountain crest in The Glen at 570m above sea level. *Jamesoniella* spp., *Rhacocarpus humboldtii* and *Thysanomitrium richardii* cover a thin crust of peat, on which some *Agrostis carmichaelii*, *Nertera depressa* and *Lycopodium magellanicum* (left centre) are rooted. Part of an Empetrum mat and a few plants of *Carex thoursii* at the bottom of the photograph, and *Leceidea* sp. encrusting the stones at top right. Quadrat site XXXI.

Mount Rowett, and of the cinders and basalt composing the rim of the Edinburgh Peak crater. In the North of the island, the rounded slopes and domes of trachyte bear feldmark communities with a higher proportion of bare rock in which the low ridges of bryophytes form shallow terraces which contour the slopes. These terraces are formed mainly of *Andraea loricata*, *A. parallela* and *Ditrichum* sp., with *Jamesoniella* spp. occupying the more level surfaces of the terraces, and *Agrostis carmichaelii* lining the edges. Such a community near the top of Expedition Peak, at 860m above sea level contains the following species within a 10-m quadrat (LXIII):

<i>Agrostis carmichaelii</i>	10%
<i>Nertera depressa</i>	++
<i>Acaena stangii</i>	+
<i>Deschampsia</i> sp.	+
<i>Ranunculus caroli</i>	+
<i>Lycopodium saururus</i>	+
<i>Andraea loricata</i>	20%
<i>A. parallela</i>	
<i>Ditrichum cf. strictum</i>	
<i>Rhacocarpus humboldtii</i>	++
<i>Psilopilum</i> sp.	++
Hepaticae (collectively)	30%
<i>Cephalozia varians</i>	
<i>Gymnomitrium stygium</i>	
<i>Herpocladium minimum</i>	
<i>Jamesoniella grandiflora</i>	
<i>J. oenops</i>	

About a quarter of the surface is bare of plants, and the flakes of rock which are strewn all over the area bear much *Placidiopsis parallina*.

In some nearby areas where the surface is kept constantly moist by seepage from the surrounding moss mats, a continuous thin covering of peat has formed over the rock, and dwarfed *Scirpus* sp. re-

places *Agrostis carmichaelii* on the edges of the terraces. *Rostkovia tristanensis*, *Deschampsia* sp., and *Apium australe* are also found in these areas.

MONTANE ROCK COMMUNITIES

North of Edinburgh Peak, at about 700m above sea level, considerable areas of trachyte are almost bare of vegetation although they are protected from the full force of the Westerly winds by the flanks of Edinburgh Peak itself. Few rock fragments are found on the surface of the smooth rounded domes, which support only small tufts of *Andraea grimmioidea* and some *Stereocaulon*, with diminutive *Jamesoniella oenops* in the rock crevices. The vegetation of these domes is essentially similar to that found on Expedition Peak, except that there is more bare rock, and the flowering plants are quite unimportant, even where an apparently suitable surface is provided for their colonisation in the bryophyte-filled crevices. A 10-m quadrat (XXXIXa) contained the following species:

<i>Lycopodium saururus</i>	++
<i>Rostkovia tristanensis</i>	+
<i>Rhacomitrium crispulum</i>	5%
<i>Andraea grimmioidea</i>	10%
<i>Lepicolea ochroleuca</i>	+
<i>Jamesoniella colorata</i>	10%
<i>J. grandiflora</i>	
<i>Adelanthus unciniformis</i>	
<i>Stereocaulon implexum</i>	+
Bare rock	about 60%

Bryophytes form a more continuous layer in the damp hollows between adjacent domes, and a few higher plants colonise these wet surfaces. A ten meter quadrat laid across the bottom of one of these hollows yielded the following species (XXXIXb):

<i>Scirpus</i> sp.	10%
<i>Carex thoursii</i>	5%
<i>Nertera depressa</i>	++
<i>Agrostis carmichaelii</i>	++
<i>Rostkovia tristanensis</i>	+
<i>Lycopodium saururus</i>	+
<i>Andraea loricata</i>	70%
<i>Jamesoniella grandiflora</i>	
<i>J. colorata</i>	
<i>Rhacocarpus humboldtii</i>	5%
<i>Blinda</i> sp.	+
<i>Lepicolea ochroleuca</i>	+
<i>Breutelia cf. plicata</i>	+

More extensive areas of bare trachyte to the North and North-East of Expedition Peak, in which the surface of the large rock domes is strewn with boulders and shattered rock debris, also have an extremely sparse plant cover. The largest of these domes, the Barren Dome, rises about 120m from the edge of the plateau, here at 600m above sea level. Deep fissures dissect the surface of the dome, and a few plants of *Dryopteris aquilina* and *Hymenophyllum peltatum* were seen in some of these. The dome surface is largely covered with flat slate-like flakes of trachyte between which are found pockets of raw mineral soil and gravel up to 10cm deep. Plant cover over the whole of the dome is extremely

sparse, and apart from crustose lichens, less than 5% of the surface bears any plants at all. Occasional tufts of *Agrostis carmichaelii* and *Deschampsia* sp. grow in sheltered crevices, and small plants of *Empetrum rubrum* and *Nertera depressa* grow in a few places. The species list for a 10-m quadrat (XXXIV) on the top of the dome at 720m above sea level was:

<i>Agrostis carmichaelii</i>	++
<i>Deschampsia</i> sp.	+
<i>Nertera depressa</i>	+
<i>Carex thoursii</i>	+
<i>Andraea grimmiioides</i>	+++
<i>Thysanomitrium richardii</i>	++
<i>Rhacomitrium lanuginosum</i>	+
<i>Psilopilum</i> sp.	+

Crustose, and some fruticose lichens are the most important plants, especially *Placidopsis fuscicula*, *Lecidea* sp. and *Stereocaulon implexum*. The blue-green algae *Gloeocapsa* and *Scytonema* were also collected from amongst lichens in this quadrat.

In the valley between the Barren Dome and Nigel's Cap, areas of bare silt are found in sheltered hollows between large rocks. This silt is evidently deposited by downwashing from the Dome, and smaller pockets of silt are found all over the Dome itself, sometimes covered in standing water. All these areas of silt are quite bare of vegetation.

The vegetation of crags and rock faces over 600m above sea level differs little from that already described for the rock domes. On the large volcanic plug of the Hag's Tooth at 660m, *Andraea grimmiioides* and *Placidopsis parallina* colonise the bare exposed rock, while *Campylopus introflexus*, *Ditrichum strictum*, *Rhacomitrium lanuginosum* and *Grammitis billardieri* are common in the crevices. The larger and more sheltered clefts in the rock, where some peat has accumulated are usually occupied by one or more of the following species: *Agrostis carmichaelii*, *Deschampsia* sp., *Carex thoursii*, *Empetrum rubrum*, *Uncinia brevicaulis*, *Blechnum penna-marina*, *Lycopodium saururus*, *Thysanomitrium richardii*, *Rhacocarpus humboldtii*, *Jamesoniella* spp., together with smaller liverworts.

THE HABITAT FACTORS AND GEOGRAPHICAL RELATIONSHIPS OF THE MOORLAND, FELDMARK, AND MONTANE ROCK COMMUNITIES

Although the degree of exposure is obviously the most important factor determining the distribution of the moorland, feldmark and montane communities, the rock type also has a marked influence, and the vegetation of the upper trachytes (LeMaitre 1960) differs considerably from that of the surrounding basalts which are similarly exposed.

In general, exposed areas of broken ground above about 600m, which provide some local shelter, subsurface drainage, and easy anchorage for mat-forming plants are dominated by moorland communities. The moorland is therefore concentrated upon the middle basalts, which weather to steep boulder-strewn slopes with some small scree formation. The

feldmark and rock communities cover more of the rounded trachyte domes, and the intruded trachyte plugs and dykes. It is difficult to account for the almost complete absence of plants on the trachyte domes North of Edinburgh Peak: they are possibly bald on top because water is not retained on the surface (which is free of deep crevices), and any potential colonists are either dried up in the short rainless spells or washed from the surface during storms. Only in the moister hollows between adjoining domes can a bryophyte mat become established. On the larger Barren Dome, the broken and crevassed surface, with plenty of available water and pockets of mineral soil, would seem to provide a suitable habitat for a *Rhacomitrium*-*Empetrum* mat, which is found in some areas at the same altitude on the Western and Southern faces of Mount Rowett. Neither climatic extremes due to altitude or exposure, nor mobility of the surface, nor the absence of suitable colonists on the Island, can be invoked to explain the almost bare surface of the Barren Dome, and it is possible that the rock is chemically unsuited to support plant growth. Analyses of the aegirine trachytes near the Barren Dome (to the North of Edinburgh Peak), and comprising the intruded plug of the Hag's Tooth, and at the head of Deep Glen, revealed 20 ppm of lead in 4 samples. On the other hand, this element was found to be absent from the intruded trachyte plug at the head of Worseley Dale and from the trachytes of Gonydale (LeMaitre 1959).

The moorland and feldmark vegetation on Gough Island resembles both structurally and floristically, the *Rhacomitrium*-*Empetrum* heath and Alpine Desert on the upper parts of the Tristan da Cunha peak, but true feldmark is more extensive on Tristan due to the greater extent of unstable volcanic cinders there, and the higher altitude.

Both the Tristan and Gough montane moorland communities resemble in their general structure some of the *Empetrum rubrum*-*Rhacomitrium* communities described from the Scottish mountains (Burgess 1951). Open feldmark communities consisting of scattered cushion-plants growing on bare and very exposed mineral soils have been described from a number of southern islands (refs. in Wace 1960), and from New Zealand (Cockayne 1928) and the Tropical American mountains (Troll 1958). Although the Gough communities are here referred to as "feldmark" they are not dominated by the large compact cushion-forming flowering plants (*Azorella*, *Raoulia*, *Haastia*) that characterise the sub-Antarctic, New Zealand and tropical American mountain communities.

PEAT BOGS

The term "bog" as used here, includes all extensive deposits of peat more than 2m deep, however formed. The two upland areas of impeded drainage—valleys and plateaux—bear different types of bog with differing vegetation.

VALLEY BOGS

The valley bottoms of Mildred Mire, Albatross Plain (Fig. 17), and Gonydale contain extensive mounds and ridges of peat up to 5m deep. There is generally no continuous "lagg" surrounding the bogs, and where a marginal drainage ditch is found it is frequently obstructed or bridged by rocks and peat which have fallen from the mountain slopes above. The drainage channels between the convex peat masses are fed with water both by surface runoff, and from subterranean channels within the peat the courses of which can be traced on the surface by the lines of "swallow holes" into which the surface waters drain.

The vegetation of the valley bogs varies according to the wetness of the peat surface, but *Sphagna* are the principal peat-forming plants and are everywhere abundant. Three valley bog communities were distinguished:

- a) The driest areas, usually concentrated towards the sides of the larger mounds, bear an *Empetrum*-*Rhacomitrium* association rather similar to that described under Moorland. Two 10-m quadrats yielded the following lists of species:

	LIV (Albatross Plain)	XXI (Gonydale)
<i>Empetrum rubrum</i>	20%	50%
<i>Tetroncium magellanicum</i>	10%	15%
<i>Scirpus</i> sp.		10%
<i>Rostkovia tristanensis</i>		++
<i>Nertera depressa</i>	+	5%
<i>Apium australe</i>		+
<i>Carex thourarii</i>		+
<i>Lagenophora nudicaulis</i>		+
<i>Deschampsia</i> sp.		+
<i>Blechnum penna-marina</i>		+
<i>Rhacomitrium lanuginosum</i>	5%	15%
<i>Sphagnum magellanicum</i>	20%	++
<i>S. fimbriatum</i>	5%	+
<i>Breutelia</i> cf. <i>plicata</i>	10%	+
<i>Dicranoloma</i> spp.	10%	++
<i>Ptychomnion densifolium</i>	+	++
<i>Dicranodontium tristanense</i>		++
Hepaticae (collectively)	10%	5%

The following Hepaticae were collected from quadrat XXI: *Anastrophyllum crebrifolium*, *Blepharidophyllum densifolium*, *Blepharostoma quadripartitum*, *Lepidozia halleana*, *L. oligophylla*, *L. saddlensis*, *L. setiformis*, *Lophocolea obvoluta*, *L. puccioana*, *Riccardia alci-cornis*. Of these two quadrats, that in Gonydale is the drier. In general, *Rhacomitrium lanuginosum* only enters the bog communities where the surface is not squelchy, and it decreases where *Sphagna* and *Jamesoniella* spp. are important, although isolated hummocks of *Rhacomitrium* are found in the wetter bogs (cf. Tallis 1958).

- b) Most of the peat surfaces in Albatross Plain are sodden, and although there are few pools water soon collects in footprints on the bog surface. *Sphagnum magellanicum* and *S.*



FIG. 17. Albatross Plain from the north-west. Dissected valley-bog peats surrounded by wet heath at the bottom of the Mount Rowett spurs. The bog is about 600m above sea level. *Agrostis carmichaelii* moorland covers the flanks of Mount Rowett in the distance. *Empetrum*-*Rhacomitrium* heath, with scattered plants of *Deschampsia* sp. in the foreground.

fimbriatum form small hummocks, the tops of which are usually occupied by *Scirpus* spp. and *Tetroncium magellanicum*. *Dicranoloma* spp. and *Breutelia* cf. *plicata* grow around the lower parts of the hummocks, and the hollows are occupied by *Jamesoniella* spp. and *Rhacocarpus humboldtii*. These hummocks and hollows are less than 15 cm from trough to crest, and about 20 cm across. They tend to form ridges which contour the slopes, and are possibly flow ridges. Lists of species are given from four 10-m quadrats in different



FIG. 18. Albatross Plain bog surface. In the foreground, low hummocks of *Dicranoloma* spp. and *Sphagnum magellanicum*, topped by *Scirpus* spp. and *Empetrum rubrum*. *Apium australe* and *Deschampsia* sp. in the swallow holes, and dark clumps of *Tetroncium magellanicum* beside the courting albatrosses (*Diomedea exulans dabbenena*) in the background. The depth of peat at the boring site (quadrat LXVII) is 4.85m.

parts of Albatross Plain (site no. LXVII is shown in Fig. 18).

	XXIV	XXXIII	LIII	LXVII
<i>Scirpus</i> spp.	10%	5%	35%	40%
<i>Tetroncium magellanicum</i>	15%	10%	10%	+
<i>Carex thourarii</i>			+	+
<i>Empetrum rubrum</i>		+		
<i>Nertera depressa</i>	+			
<i>Rostkoria tristanensis</i>			+	
<i>Uncinia compacta</i>			+	
<i>Sphagnum magellanicum</i>	60%	45%	30%	15%
<i>S. fimbriatum</i>	5%	25%	5%	
<i>Dicranoloma</i> spp.	+	5%	+	20%
<i>Breutelia</i> cf. <i>plicata</i>		5%	5%	
<i>Rhacocarpus humboldtii</i>			+	5%
<i>Thysanotrium richardii</i>		+		
Hepaticae (collectively)	++	5%	10%	15%

These 4 quadrats illustrate the change in vegetation with the increasing abundance of *Sphagnum* spp. in the wetter places, where *Tetroncium* becomes more widespread, the Hepaticae less conspicuous, and *Empetrum* disappears.

- e) Some of the valley-bog peat masses have small flat areas on the tops of the convex mounds where *Sphagna* grow more or less submerged in very wet "scraw bog" (Webb 1947). Two 10-m quadrats in such places yielded the following lists of species:

	X (Gonydale)	LXVIII (Albatross Plain)
<i>Scirpus</i> spp.	5%	30%
<i>Tetroncium magellanicum</i>	+	
<i>Sphagnum magellanicum</i>	90%	60%
<i>S. fimbriatum</i>	+	10%
<i>Ptychmion densifolium</i>	+	
<i>Drepanocladus</i> sp. (?)	+	

These very wet areas merge in places into extensive shallow tarns overlying a layer of *Jamesoniella* spp., and fringed by *Scirpus* sp.

PLATEAU BOGS

The plateaux at 600-700m above sea level, which surround the highest peaks, bear a different type of bog vegetation to that of the mountain valleys. The peat is shallower than in the valleys, and forms broad flat expanses, and although much of the drainage is subterranean (several streams draining the flanks of Edinburgh Peak disappear beneath the peat of Tarn Moss), the surface is always very wet, and the water seeps down the gentle gradient over the shallowly terraced vegetation to the edges of the plateaux. The greatest depth of peat found during extensive probings of Tarn Moss was two metres.

Sphagna, although present, are less important in these bogs than in the valleys, and *Dicranoloma* spp., *Rhacocarpus humboldtii* and Hepaticae form the bulk of the vegetation. The peat formed is more humified than the valley bog peat, and has fewer fibres. The surface is more or less terraced in shallow steps a few centimetres high, with the bryophytes covering the wet flat surfaces and *Scirpus*

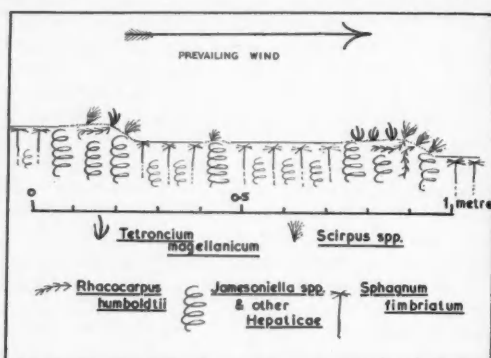


FIG. 19. Surface vegetation on Tarn Moss plateau bog. Ridges mainly of Hepaticae and *Rhacocarpus humboldtii*, surmounted by dwarf *Scirpus* sp. and *Tetroncium magellanicum*, with *Sphagnum fimbriatum* mainly in the hollows.

spp. and *Tetroncium magellanicum* growing on the drier edges and faces of the steps (Fig 19).

The 10-m quadrats on Tarn Moss yielded the following species:

	XXXVII	XL
<i>Scirpus</i> spp.	++	50%
<i>Tetroncium magellanicum</i>	30%	5%
<i>Agrostis carmichaelii</i>	+	
<i>Rostkoria tristanensis</i>		+
<i>Nertera depressa</i>	+	
<i>Sphagnum fimbriatum</i>	20%	20%
<i>S. magellanicum</i>		+
<i>Dicranoloma</i> spp.	10%	5%
<i>Rhacocarpus humboldtii</i>	15%	++
<i>Breutelia</i> cf. <i>plicata</i>	+	+
Hepaticae (collectively)	20%	15%

The following Hepaticae were collected from quadrat XXXVII: *Anastrophyllum crebrifolium*, *Blepharidophyllum densifolium*, *Blepharostoma quadripartitum*, *Jamesoniella grandiflora*, *Lepidozia saddlensis*, *Lophocolea subcapillaris*, *Riccardia alcicornis*, *R. mucophora*, *R. nudimitra*, *R. pallidivirens*, *Schistochila pachyphylla*.

There are a number of shallow tarns amongst the bogs on the plateaux. These are generally fringed by a dense growth of *Scirpus* spp., but they contain no aquatic vascular plants. Along their inner margins, the plateau bogs grade into the surrounding *Agrostis carmichaelii* moorland, as the peat thins out on the mountain slopes. There is generally no "lagg" ditch.

BOG STREAMSIDES

Between the mounds of peat on Albatross Plain and Gonydale, and on the margins of some of the plateau bogs, the drainage streams are surrounded by a mixed fen-like vegetation which is dominated by *Carex insularis*, *Apium australe* and *Deschampsia* sp., growing to a height of about 1m, on re-distributed peat which is loosely-compacted and has a gritty texture. These streamside communities are rather similar to the Grass and Sedge Heath, already

described, and into which they merge in the mountain gullies surrounding the bogs. But they differ from the Wet Heath community principally in the importance of *Carex insularis* (which often forms pure stands several square metres in extent), and in the presence of *Glyceria* sp. in the streamside communities. *Sphagna* are absent or quite unimportant beside the bog streams.

The areas studied lay on the eastern fringe of the Gonydale bog (XXII) at 480m, and on Albatross Plain (LXI) at 600m above sea level beside the main drainage stream at the centre of the bog. In both areas the peat under the quadrat is from 0.5 to 1m deep, and full of grit and stones. The species found in two 10-m quadrats were:

	XXII	LXI
<i>Carex insularis</i>	35%	25%
<i>Apium australe</i>	30%	10%
<i>Scirpus</i> spp.	10%	5%
<i>Ranunculus caroli</i>	10%	5%
<i>Deschampsia</i> sp.	5%	20%
<i>Carex thouarsii</i>	+	5%
<i>Uncinia brevicaulis</i>	+	+
<i>Agrostis media</i>		++
<i>A. carmichaelii</i>		15%
<i>Glyceria</i> sp.		5%
* <i>Poa annua</i>		++
<i>Acaena sarmentosa</i>	++	
<i>Hydrocotyle leucocephala</i>	++	
<i>Blechnum penna-marina</i>	5%	10%
<i>B. palmiforme</i>	+	+
<i>Rumohra adiantiformis</i>	+	
<i>Asplenium alvaradense</i>	+	

Brachythecium subplicatum and *Ptychomnion densifolium* cover much of the peat beneath the vascular plants.

The wandering albatross (*Diomedea exulans dabbenena*) nest in this type of vegetation in and around the bogs. Their nests are generally surrounded by a heavily trampled area in which small clumps of *Scirpus* sp. and a carpet of *Brachythecium subplicatum* are the most abundant plants. **Poa annua* was noted from several such nesting sites in Albatross Plain, but is elsewhere very infrequent away from the coasts and penguin rookeries.

THE DEVELOPMENT AND RELATIONSHIPS OF THE BOG-FORMING COMMUNITIES

The constantly wet oceanic climate of Gough Island promotes a rapid growth of peat, which blankets much of the rock. The restriction of deep peat deposits to the mountain valleys and plateaux is principally due to the steep and rugged terrain elsewhere on the island preventing peat accumulation.

Much of the peat upon which the Fern Bush and Wet Heath formations are developed could truly be described as "blanket bog," in the sense that the peat growth occurs independently of the local drainage conditions, and is therefore a true climatic climax development "depending on high rainfall and very high average atmospheric humidity" (Tansley 1939). Ombrogenous peat with extensive *Sphagnum* cover and a typical domed and dissected topography is found only in the mountain valleys and on some of

their surrounding slopes. Structurally, these Gough Island valley bogs resemble the high level bogs of Britain (Pearsall 1950), the "ombro-soligenous" bogs of Southern Sweden (von Post 1937), and the "mixed mires" of Ireland (Osvold 1949). They are also essentially similar in structure and vegetation to Soggy Plain, Tristan da Cunha (Wace & Holdgate 1958). Floristically they resemble the "Weissmooren" of Tierra del Fuego (Roivainen 1954), especially in the importance of *Sphagnum magellanicum* and *Tetroncium magellanicum*, and the presence in the drier parts of *Empetrum rubrum*.

The flat-topped peat masses on the Gough Island plateaux, in which *Sphagna* are less important, and which are less dissected than the valley peats, are probably mainly soligenous in origin, since they are over-run by water flowing off the peaks. They apparently resemble the "Bryales Bogs" of Western Patagonia (Auer 1958), and the "Braunmooren" of Fuegia (Roivainen 1954), especially in the importance of bryophytes other than *Sphagna* in their composition.

None of the Gough Island bogs displays a mosaic of hummocks and hollows which are said to be characteristic of the actively growing parts of raised bog in Britain (Tansley 1939) in the "regeneration complex." Nor did the single peat profile investigated (on Albatross Plain, near site LXI) show any sign of such a system having been present in its very uniform stratigraphy. The surface corrugations on the bogs on Gough are on a far smaller scale than the hummocks and pools of the regeneration complex, and there is no sign of upgrowth in the pools or decay of the hummocks, even where the water table is near enough to the surface to flood the hollows. Unevenness of the surface, and ridge formation, is usually related to the slope of the underlying peat masses in the Gough bogs.

It is probable that the Gough Island bogs are now actively growing. Carbon-dating of the peat profile on Albatross Plain suggests that growth has been at the rate of 7.7 cm per century since the deposition of a layer of volcanic ash 2345 (± 120) years ago. The upland peat deposits are not at present eroding significantly; nor are there any signs of bog bursts having occurred recently. Apart from the avalanching of deposits on steep slopes due to peatslip, active peat erosion was only noticed on any scale at the North end of Tarn Moss.

DISCUSSION

THE VEGETATIONAL HISTORY OF GOUGH ISLAND

Gough Island is at present surrounded by water of over 2000m depth (Stocks 1933). It is therefore unlikely that it has ever been connected by land to the islands of the Tristan da Cunha group, or to the surrounding continents. Although there is as yet no geochemical or paleomagnetic evidence to give any direct indication of its age, it probably emerged from the sea in late Tertiary times (Le-Maitre 1960). The presence of a layer of volcanic

ash, which almost certainly originated from the island itself, in the carbon-dated Albatross Plain peat (see p. 3, p. 39), shows that volcanic activity certainly took place as recently as about 2400 yrs ago. The absence of any signs of glaciation in the island also suggests that (at least in its present form) Gough Island is very young.

The absence of past land connections, and the youth of the present island biota, is supported also by evidence from the biology, relationships and size of the present flora and fauna. This biological evidence, which is more fully discussed elsewhere (Holdgate 1960, Wace 1960, & in preparation), may be summarised as follows:

- a) The flora and fauna both show the characteristics of those of a truly "oceanic" island (Wallace 1895) in that they are very poor in numbers of native species, and many groups are entirely absent. There are, for example, only 32 species of native flowering plants, and 7 beetles native to the island, and no reptiles, fresh-water fish or gymnosperms.
- b) The disseminules of the native vascular plants are almost all easily-dispersed over long distances by wind, or are adapted to carriage by animals or water (Wace 1960); and the proportion of spore-dispersed pteridophytes to seed-dispersed flowering plants (27/32) is high. The same principle of relative ease of long-distance dispersal is also true of the native fauna (Holdgate 1960).
- c) There are no genera of plants endemic to the island, and all the species which have hitherto been described as "endemic" are very similar to continental or circum-Antarctic species. The same principles have been found to apply *mutatis mutandis* to the invertebrate fauna (Holdgate 1960).

(a) and (b) suggest that the island species reached Gough Island across the sea, and (c) that they are recently immigrant.

The pollen content of the peats in Albatross Plain has remained remarkably constant since peat formation started there (Hafsten 1960a, 1960b). The lowest layers of peat from an excavated monolith 2.2m deep, and lying directly on the rock (near site LXI) have been dated at 4720 (\pm 130) yrs before the present (Godwin & Willis 1959). From a comparison of the pollen content of this lowest dated peat layer to that of the deeper pollen-analysed profile, Hafsten (1960b) concluded that the vegetation and flora of the island have undergone no major changes during the last 5000 yrs.

The only pollen or spores in the Albatross Plain peats that do not belong to plants at present growing on the island, have been accounted for either by long distance pollen transport from South America (*Ephedra* spp., *Nothofagus*), or by temporary colonisation of the island (?*Collomia*), or by contamination of the analysed peat samples in the laboratory

(*Pinus*, *Betula*, *Alnus*, *Corylus*). Apart from the single doubtful case of *Collomia*, there is no evidence that any plant species that is not present on Gough Island today, formerly grew there.

It is clear that Gough Island has taken much longer to reach its present deeply dissected state, than the 5000 yrs or so that have elapsed since the deepest-found deposits of peat were laid down. It is therefore probable that the remains of any previous vegetation have been destroyed by recent volcanic action or removed in an erosive process. Its deep dissection and general physiography suggest that Gough Island is about the same age as Masafuera and St. Helena, both of which have a high proportion of endemic species and some endemic genera in their native floras (Skottsberg 1956, Wallace 1895). The absence of endemics on Gough possibly indicates therefore that the present vegetation is much younger than the island itself.

HUMAN INFLUENCE ON THE VEGETATION

The ecosystems of remote islands are liable to rapid change and the replacement of their native species by introduced aliens, when their biological isolation is broken down by the activities of man. Their vulnerability is due fundamentally to the evolution of their biota in isolation from grazing and predatory mammals, and to the small size of their native floras and faunas whose species have been selected primarily for their capacity to achieve long-range dispersal, and not for their ability to withstand competition from continental species (Elton 1958, Holdgate & Wace 1961).

Gough Island is almost unique amongst the oceanic islands of temperate latitudes in having its native vegetation substantially unaffected by human interference. Only a small area immediately surrounding the meteorological station at Goncalo Alvarez, and parts of the narrow strip of level ground at the foot of the cliffs opposite Lot's Wife, had been cleared of Phylea by 1956; and there was only one known case of the firing of the vegetation by that date, when some coastal tussock grassland was burnt near Lot's Wife Cove in 1953 (Forsyth Thompson 1956). No land mammals, reptiles or amphibians are native to the island. Until 1956 none had been introduced except for mice (*Mus musculus*) which were probably brought by sealers in the last century, and although abundant over most of the island, they have a negligible effect on the plant life. Of the 12 flowering plants which had been introduced by man up to 1956, *Agrostis stolonifera*, *Holcus lanatus*, *Poa annua*, *Rumex obtusifolius*, and *Sonchus oleraceus* are spreading aggressively into the native vegetation inland (especially on to the sites of peatslips), and *Stellaria media* and *Plantago major* are common in penguin rookeries round the coasts.

With the establishment of a permanent meteorological station on the island in 1956, the importation of sheep and poultry, and the regular visits of ships supplying the station, man can be expected to have

an increasing influence on the vegetation in future. It is therefore important to assess what some of these effects might be. Sheep have rapidly destroyed *Poa flabellata* in the immediate vicinity of Goncalo Alvarez weather station (Stableford 1958), and above the shore in the Bay to the North of Dell Rocks, but they are confined to these areas by cliffs or very steep slopes. If they were once let loose on the southern slopes near Transvaal Bay (where it was intended to re-establish the meteorological station in 1961), and from where they could reach the extensive *Poa flabellata* communities of the Western and Northern cliffs, widespread devastation of these coastal tussock communities would certainly follow, with the consequent destruction of the associated communities of ground-nesting birds and accelerated erosion of the underlying rock. Such destruction of similar island tussock grass communities as a result of sheep grazing has been reported from the Falkland Islands (Davies 1939) and from some of the New Zealand Shelf islands (Oliver & Sorensen 1951). The importation of any other grazing mammals (especially rabbits) would have a similarly catastrophic effect on the vegetation, especially on the tussock grasslands. Other factors tending to eliminate the dominant species of Fern Bush or Tussock Grassland, or to loosen the peat on the steep slopes (e.g. trampling) would probably increase the frequency of peatslips, and any firing of the vegetation would undoubtedly have this effect, and could easily lead to peat fires such as swept the island of Madeira from 1425-32 (Biddle 1901).

The effects on their native vegetation of human settlement, and the introduction of grazing animals, are seen in the diminishing forests of South Trinidad (Knight 1880), Juan Fernandez (Skottsberg 1954), Hawaii (Campbell 1933, Skottsberg 1934), New Zealand (Clark 1949), and elsewhere (Elton 1958, Holdgate & Wace 1961). The end result is seen in the wrecked native vegetation and widespread soil erosion on St. Helena (Wallace 1895, Colonial Office Report 1954). There is no reason to doubt that the hitherto isolated ecosystem of Gough Island is any less vulnerable to changes induced by human activities, than in these islands.

THE INTER-RELATIONSHIPS AND PHYSIOGNOMIC AFFINITIES OF THE VEGETATION

From the foregoing accounts, it is clear that the Gough Island vegetation is cool temperate and sub-Antarctic in character. The inter-relationships of the principal communities are summarised in Fig. 20, from which it is seen that degree of exposure, as well as altitude are the prime factors which are correlated with the distribution of the different formations. Rock types are important in influencing the vegetation mainly in so far as they have given rise to differing topographies on weathering. Biotic factors are important principally around the coasts, due to the gregarious breeding of seals and penguins, but the peat-burrowing activities of the ground-nest-

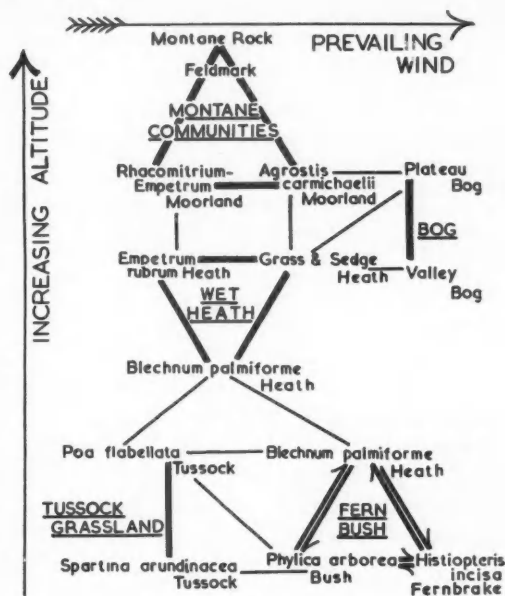


FIG. 20. Diagram to illustrate the inter-relationships of the principal communities comprising the Gough Island vegetation.

ing *Procellariidae* are also important in aerating and loosening the peat inland.

In general, the formations with structural similarities to sub-Antarctic vegetation are concentrated on the windward side of the island, while those of temperate (verging to sub-tropical) affinities are mainly on the leeward side, or in sheltered situations.

In a review of the botany of the Southern Islands (Wace 1960), a classification was proposed by vegetation types in which the Tristan-Gough archipelago is grouped with the Falklands, the New Zealand shelf islands and the New Amsterdam-St. Paul group, as temperate, and the more southerly islands without any fern bush vegetation as sub-Antarctic or Antarctic. The vegetation of Gough Island in relation to that of other temperate islands and South-Western Chile, is considered below.

TRISTAN DA CUNHA GROUP (37°S, 12°W)

Gough Island lies only 370 km South South-East of Tristan da Cunha, and their climates are similar, although Gough is both colder and wetter than Tristan. The flora and vegetation of the 2 islands is also similar: the altitudinal zonation of their native formations is compared in Fig. 21, from which it is seen that the transitions between corresponding formations are about 150 to 300m higher on Tristan than on Gough.

Tristan retains its conical shape, and is less deeply eroded and therefore probably younger than Gough, and the mainly basaltic lavas on Tristan are more friable than the Gough trachytes. The plateau

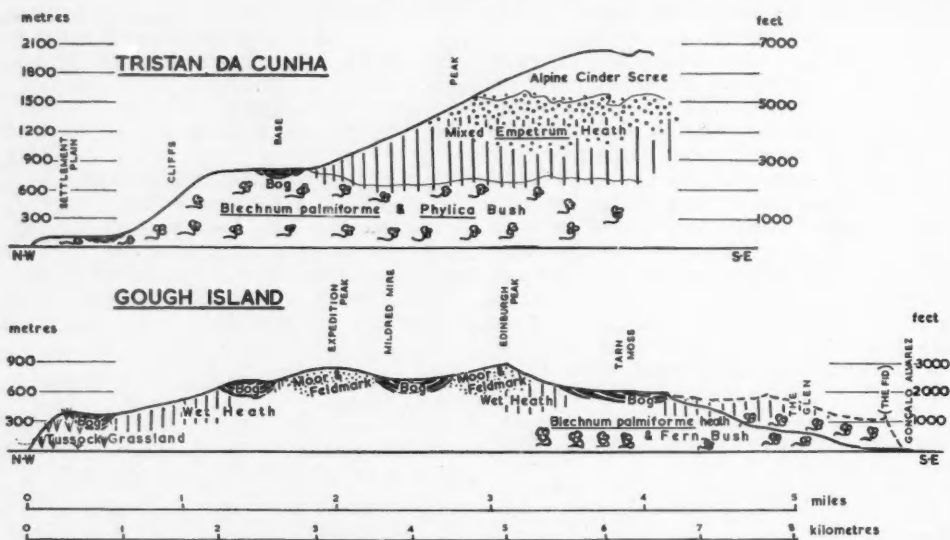


FIG. 21. Representative sections of Tristan da Cunha and Gough Island drawn to the same scales, showing the zonation of their native vegetation types. Horizontal and vertical scales equivalent.

at 600m above sea level which is present on both the islands, supports few bogs on Tristan, probably because there are no open valleys, and the porous rock is more broken up by gulches draining the central peak. The extensive wet heaths of Gough have their counterpart on Tristan in the widespread *Blechnum palmiforme* scrub covering the more level ground, and this gives way to well-developed bog only in the few places where drainage from the Peak is impeded against the sides of subsidiary volcanic craters. Tristan is more than twice the height of Gough, and there is no counterpart on Gough to the Alpine Desert and cinder scree of the upper reaches of the Tristan peak (Wace & Holdgate 1958).

Human interference and settlement on Tristan has produced the most striking differences between the vegetation on the 2 islands. The lesser importance of *Phyllica* and the absence of extensive areas of tussock grassland on Tristan may be due both to the effects of clearance by man or elimination by human-imported animals, and the presence of a zone of *Rumex acetosella* on the lower parts of the Tristan peak has resulted from the human introduction of that plant to the island (Wace & Holdgate 1958). The presence of grassland on the lowland plains of Tristan is also due to clearance by man, and the grazing of imported animals.

The vegetation of the uninhabited Nightingale and Inaccessible Islands, near Tristan, has never been fully described, but from the fragmentary references in Hafsten (1951), Hagen (1952), Christophersen (1940), and the accounts of the Tristan islanders, it seems that Nightingale is largely cov-

ered in dense *Spartina arundinacea* tussock grassland similar to that found on Penguin Island, but with some open water and boggy ground (Hafsten 1960b). Its vegetation probably resembles also that of some parts of the southern slopes of Gough near South Point. Inaccessible Island has a boggy plateau at about 600m above sea level, with a considerable growth of *Phyllica*. Domes of trachyte which are bare of vegetation, reminiscent of similar features on Gough are figured by Dunne (1941).

In general, the native vegetation of the Tristan-Gough archipelago varies only in detail from one island to another according to their different topographies. Apart from the sub-Antarctic and temperate *Poa flabellata* tussock grass formation of Gough Island, all the native formations of Gough are represented in the Tristan group islands, with few physiognomic or floristic differences.

NEW AMSTERDAM—ST. PAUL GROUP (38°S, 77°E)

These 2 volcanic islands in the Indian Ocean at about the same latitude as Gough, but 7400 km distant, have many floristic similarities to the Tristan-Gough group, and their vegetation and flora have been compared to that of Tristan (Hemsley 1885, Hooker 1875, Schenck 1903). Detailed vegetational descriptions have not been published, but the dense *Poa novaeae*, *Spartina arundinacea*, and *Scirpus* sp. tussock on the sides of the St. Paul crater and penguin rookeries apparently resembles the maritime tussock grassland of Gough. The *Phyllica* bush, wet heath and bog of Amsterdam Island appears from photographs to be similar to the same formations on Gough and Tristan (Amstutz de la Rue 1954), but has been damaged by cat grazing.

FALKLAND ISLANDS (52°S, 60°W)

These continental islands are colder than Gough, and although *Hebe elliptica* there forms small thickets (Skottsberg 1913) similar to *Phylica arborea* on Gough, there is no extensively developed equivalent of the Gough fern bush formation. Maritime tussock grassland, wet oceanic heath, and *Empetrum rubrum* moorland in the Falklands all resemble their Gough counterparts both floristically and structurally, but the Falkland bogs are dominated by the cushion-forming flowering plants *Donatia*, *Gaimardia*, and *Astelia pumila*. *Sphagnum* spp. are absent or unimportant. The cushion-forming feldmark species of the Falklands (*Azorella selago*, *Bolax gumifera*) are also absent from Gough, and although *Empetrum rubrum* on Gough sometimes assumes a very compact pulvinate form, there are no true equivalents of the same life form as the Falkland plants. Nor is there any equivalent on Gough to the *Cortadiera pilosa* grass steppe of the Falklands.

NEW ZEALAND SHELF ISLANDS (48°-53°S, 166°-180°E)

Structural equivalents of all the Gough Island formations are found in these continental islands, with which they also share many similar or closely-related circum-Antarctic species (Wace 1960). The principal dominant of fern-bush in the New Zealand shelf islands (*Metrosideros lucida*) is genetically unrelated to *Phylica arborea*, but it dominates physiognomically similar communities with a wider

variety of associated species than on Gough. The maritime tussock and wet heath formations in the New Zealand shelf islands are also physiognomically similar to their Gough Island counterparts, but the sub-Antarctic herbfield communities which are dominated by large-leaved rosette plants, and the feldmark communities which are dominated by cushion-forming flowering plants, have no genetic and only slight physiognomic resemblances to Gough Island communities. All the islands south of New Zealand, unlike Gough, have suffered Quarternary glaciations (Speight 1909), and although their coasts are precipitous they are less rugged inland than Gough, and their less broken terrain supports a greater proportion of windswept wet heath and bog.

JUAN FERNANDEZ GROUP (34°S, 79°-81°W)

The vegetation of these 2 sub-tropical islands bears some resemblance to that of Gough Island. Masafuera is topographically similar to Gough, and its upper vegetational formations are similarly disposed (Fig. 22). The Masafuera West coast cliff grassland, Eastern "quebrada" upper forest, and upland oceanic heath, are all somewhat similar in their general physiognomy to the Gough maritime tussock, fern bush, and wet heath respectively. In particular, the field layer of *Lophosoria quadripinnata*, *Polystichum berterianum*, *P. vestitum*, *Histiopteris incisa* and *Dryopteris inaequifolia* beneath the shrub-like trees (Skottsberg 1953), is reminiscent

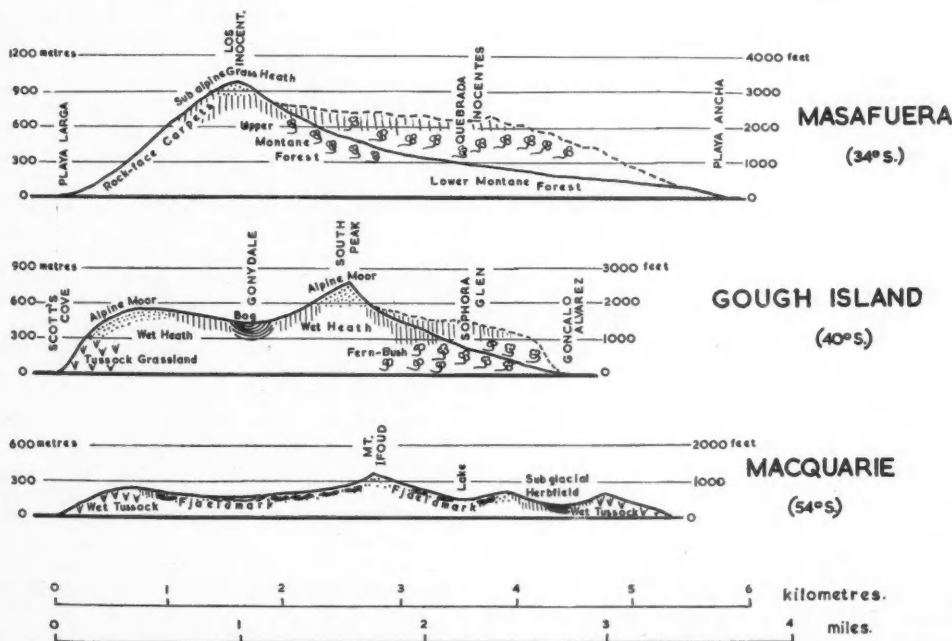


FIG. 22. Vegetational profiles of 3 southern islands, plotted on the same scales, vertical axes not exaggerated. Structurally similar vegetation types are represented by identical symbols in the different islands. The profiles are constructed on west-to-east topographical sections, so that their winward sides lie to the left of the diagram. Data for Masafuera from Skottsberg (1953), and for Macquarie from Taylor (1955).

of the *Blechnum palmiforme*, *Histiopteris incisa* and *Dryopteris aquilina* field layer of the Gough Island fern bush. The lower forest of the Juan Fernandez Islands, with a high proportion of endemic species, rosette trees, and woody Compositae, have nothing in common with the Gough Island vegetation, and are probably the descendants of an ancient vegetation which has never inhabited the remoter and more recently colonised mid-Atlantic islands.

FUEGIA & SOUTHERN CHILE, SOUTH OF 48°S

The resemblances of the Gough Island wet heath to the magellanic moorland of South-Western Chile (Godley 1960) have already been pointed out. Structural counterparts of the maritime tussock grass, and the feldmark formations of Gough are also found in this area, but Sphagnum bogs and fern bush are absent. Cushion-forming flowering plants are the most important peat-forming plants in the bog and wet heath formations. Floristically, however, Gough Island shares many circum-Antarctic species with South-Western Chile and Fuegia, from which area the present Gough Island flora has probably been recruited (Wace 1960 and in preparation).

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Dr. C. Blom	grasses
Mr. J. Lewis	monocotyledons
the late Mr. A. G. H. Alston	pteridophytes
Dr. D. H. Dalby	mosses
Mr. A. H. Norkett	mosses
Dr. S. Arnell	hepatics
Mr. R. Ross	fresh-water algae
Mrs. F. L. Balfour-Browne	fungi
Mr. P. James	lichens

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SUMMARY

Gough Island is a rugged volcanic island in mid-South Atlantic, about 15 km long, 8 km broad, and rising to 910m above sea level. It erupted about 2300 yrs ago, but has not been active in historical times. It has a temperate and highly oceanic climate, with a mean annual air temperature at sea level of 11.7°C, and a rainfall of 3225mm. It was discovered in about 1505, but was not permanently settled by man until 1955, when a weather station was established.

The indigenous vegetation remains almost untouched by the effects of man, and consists of 5 formations, each comprising several formations:

1. Tussock Grassland—a maritime community covering the western and northern cliffs and the penguin rookeries, consisting of large tussocks growing to c. 3m in height
 - a) *Poa flabellata* tussock
 - b) *Spartina arundinacea* tussock
2. Fern Bush—scrub-thicket, dwarf tree-fern and dense cryptogamic epiphyte forest covering most of the ground below 450m in the Eastern valleys and southern slopes
 - a) *Histiopteris incisa* fernbrake
 - b) *Blechnum palmiforme* heath
 - c) *Phyllaea arborea* bush
3. Wet Heath—stunted tree-fern, dwarf shrub, grass and sedge heath, often with thick bryophyte cover inhabiting the more sheltered ground between 450m and 700m above sea level
 - a) *Blechnum palmiforme* heath
 - b) *Empetrum rubrum* heath
 - c) Grass and Sedge heaths
4. Moorland, Feldmark & Montane Rock—mat-forming and dwarf tussock grass vegetation, verging to open bryophyte and lichen communities on the most exposed rock above 600m.
 - a) *Rhacomitrium-Empetrum* moorland
 - b) *Agrostis carmichaelii* moorland
 - c) moss-hummock and dwarf tussock feldmark
 - d) lichen communities and scattered plants on montane rock
5. Peat Bogs—peat deposits of two or more metres depth on the mountain valleys and plateaux
 - a) ombrogenous Sphagnum valley-bogs
 - b) soligenous Bryales-Hepaticae plateau-bogs
 - c) bog streamside communities of grasses and sedges

The islands has never any land connections with the continents, and pollen analyses have shown that the present vegetation has been stable for about the last 5000 yrs, and no signs of any vegetation previous to this have been found.

Comparisons of the vegetation with that of other southern islands shows that the Gough Island formations are structurally similar to sub-Antarctic, cold temperate and sub-tropical montane vegetation elsewhere. Although man has had little effect on the plant life so far, the vegetation is highly vulnerable to man's activities.

A vascular plant flora of 32 native, and 12 introduced flowering plants, and 27 pteridophytes is listed.

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APPENDIX

THE VASCULAR FLORA OF GOUGH ISLAND

The following list includes all species of vascular plants which had been recorded from Gough Island until May, 1956. Further species have probably established themselves on the island since the setting up of a permanent meteorological station then.

Plants collected in 1955-56 have been named by the systematists acknowledged elsewhere. Specimens collected by the author which have not been checked by a systematist are listed under the names of any previous Gough or Tristan records, and their names are included in parentheses.

A comprehensive Flora of Gough Island is in preparation by the author. The first set of all the specimens collected in 1955-56 has been deposited in the British Museum (Natural History), London.

Ranunculus caroli Christophersen)
Cardamine glacialis Forst.
Chenopodium tomentosum Thouars
Phytolacca arborea Thouars
Sophora macnabiana Grah.
Acaena sarmentosa Carmichael
A. stangii Christophersen
Callitriche christensenii Christophersen
C. cf. obtusangula
(Hydrocotyle leucocephala Cham. et Schlecht.)
Apium australe Thouars
Rumex frutescens Thouars
Empetrum rubrum Vahl
Nertera granadensis (Mutis) Druce
(Cotula goughensis Rudmose Brown)
(Gnaphalium pyramidale Thouars)
Lagenophora nudicaulis (Comm.) P.Dus.
Tetroncium magellanicum Willd..
Rostkovia tristanensis Christophersen
Scirpus sulcatus Thouars
S. thouarsianus Schult.
Carex insularis Carmichael
C. thouarsii Carmichael
Uncinia brevicaulis (Thouars) Thouars

- U. compacta* R. Brown
Agrostis media Carmichael
A. carmichaelii J. A. & J. H. Shult
A. sp. nov. (cf. *A. magellanica* Lam.)
Deschampsia sp. nov.
Glyceria sp. indet.
Poa flabellata (Lam.) Hook. fil.
Spartina arundinacea (Thouars) Carmichael
* (*Stellaria media* (L.) Vill.)
* (*Rumex obtusifolius* L.)
* (*R. acetosella* L.)—single specimen introduced 1955,
and subsequently destroyed.
* (*Solanum tuberosum* L.)
* (*Plantago major* L.)
* (*Hypochaeris glabra* L.)—not found 1955-56.
* (*Sonchus oleraceus* L.)
* (*Agrostis stolonifera* L.)
* (*Dactylis glomerata* L.)
* (*Holcus lanatus* L.)
* (*Poa annua* L.)
* (*P. pratensis* L.)
Lycopodium diaphanum Sw.
L. insulare Carmichael
L. magellanicum Sw.
L. saururus Lam.
Ophioglossum opacum Carmichael
Hymenophyllum aeruginosum (Poir.) Carmichael
H. peltatum (Poir.) Desv.
Adiantum poiretii Wikstr.
Asplenium alvaradense Rudmose Brown
A. insulare Carmichael
A. obtusatum Forst.
Blechnum palmiforme Christensen
B. penna-marina (Poir.) Kuhn
B. punctulatum Sw.
Dryopteris aquilina (Thouars) C. Chr.
D. paleacea (Sw.) C. Chr.
Elaphoglossum hybridum (Bory) Brack.
E. laurifolium (Thouars) Moore
E. succisifolium (Thouars) Moore
Grammitis billardieri Willd.
Gymnogramma cheilanthoides Sw.
Histiopteris incisa (Thunb.) J. Sm.
Hypolepis rugosula (Lab.) J. Sm.
Polystichum mohroides—not found 1955-56
Rumohra adiantiformis (Forst.) Ching
Thelypteris tomentosa (Thouars) Alston ined.
Vittaria vittarioides (Thouars) C. Chr.